Intra- and Intersexual Selection on Men: Their Relative Importance and Hormonal Underpinnings

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Nicki

Ohne euch wäre diese Dissertation nicht zustande gekommen.

Table of Contents

1. Preface

This dissertation is not a cumulative, publication-based dissertation, but follows it in form. It includes two manuscripts, of which one is under review and one has been submitted.

Kordsmeyer, T., & Penke, L. (under review). Effects of male testosterone and its interaction with cortisol on self- and observer-rated personality states in a competitive mating context. *Journal of Personality and Social Psychology.*

Kordsmeyer, T., Hunt, J., Puts, D. A., Ostner, J., & Penke, L. (under review). The relative importance of intra- and intersexual selection on human male sexually dimorphic traits. *Evolution and Human Behavior.*

2. Introduction

Throughout human evolution, competition with conspecifics has been and still is ubiquitous amongst humans and one major mechanism for distributing resources, such as food, territory and mates. Consequently, success in competition is an important determinant of an individual's fitness and as such at the core of Darwin's 'struggle for existence' (1871; see also Spencer, 1864). According to evolutionary psychology, many facets of competitive behaviour have been adaptive over human evolution, as success in competition was a large influence on evolutionary fitness. Aside from competing with other species, there are two kinds of competition humans engage in: intrasexual (i.e., same-sex: men vs. men and women vs. women) and intersexual (i.e., opposite-sex: men vs. women) competition. The former has been defined as "rivalry with same-sex others over access to mates" (p. 37, Buunk & Fisher, 2009). Besides access to mates, intrasexual competition is seen as a mechanism for allocating food, territory or social status (Hill, Bailey, & Puts, 2017). Intersexual competition is especially prevalent in mate choice decisions (e.g., Kokko, Brooks, Jennions, & Morley, 2003) and in between-sex conflicts such as parental investment in offspring (Trivers, 1972). Intrasexual and intersexual competition constitute the two primary components of sexual selection in humans (besides the purportedly less influential mechanisms of scrambles, sexual coercion, and sperm competition; Puts, 2016). Sexual selection is an important mechanism of natural selection and was first proposed by Darwin (1859, 1871; later developed by Fisher, 1930). It is assumed to have a major influence on the development of men's traits, and especially secondary sexual characteristics, such as beards, deep voices, and robust faces (Puts, 2016).

When comparing competition in men and women contemporarily and throughout human evolution, its prevalence purportedly is higher in men (Archer, 2009; Puts, 2016). This can be mainly ascribed to men's larger reproductive variance (Bateman's principle; Bateman, 1948), which has been estimated to be 2-4 times as large as women's in traditional societies (Puts, 2016). This has predominantly been attributed to women's higher investment in offspring (e.g., larger gamete size and lactation; Trivers, 1972). Consequently, the operational sex ratio (OSR; number of sexually active men relative to fecund women) is considerably biased towards more men (Hill, Bailey, & Puts, 2017). Insofar, these arguments suggest a higher intensity of competition in men than in women.

Endocrinological perspective

A mechanism contributing to sex differences and within-sex variations in competitiveness and related behaviours is the endocrinological system with its main messengers, hormones. Beach (1974) defined the endocrinological system as "an integrated, finely tuned coordinating mechanism sensitive to changes in both the internal and external environment and adapted to promotion of the physiological and behavioral effectiveness of the total organism" (p. 15). Hormones are predominantly released throughout the body by endocrine glands (pituitary-, thyroid-, adrenal-, pineal glands, pancreas, placenta, ovaries and testes, and directly by the brain; Carré & Moreau, 2014) into the general circulation, acting as chemical coordinators of multiple physiological and behavioural processes simultaneously (Roney, 2016) with both short- and long-distance effects via the bloodstream (Carré & Moreau, 2014). Besides slower genomic effects via intracellular androgen receptors, hormones can have rapid effects on cognition and behaviour via non-genomic pathways (Michels & Hoppe, 2008). For instance, Scheele and colleagues (2012) investigated effects of intranasal administration of the neuropeptide oxytocin (OT) on how much personal distance men (N = 57[1]) kept during a subsequent first encounter with an attractive woman. It was shown that men in monogamous relationships, but not single men, kept a greater distance to the opposite-sex member after receiving OT administration. This may be interpreted as OT supporting the maintenance of partnered men's relationships (of course, I shall acknowledge that the validity of such OT administration studies is under scrutiny; for a critical review see Leng & Ludwig, 2016). Generally, the endocrine system and hormones are relevant from an evolutionary perspective, because some hormones are highly conserved across nonhuman and human animal species, and related to evolutionarily important behaviours crucial for

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[1] Sample sizes for reported findings are added to support the reader in assessing results' robustness.

survival and reproduction such as risk-taking, aggressiveness and mate-seeking (Carré & Moreau, 2014).

One major endocrinological pathway in competitive contexts is the hypothalamus pituitary gonadal (HPG) axis, with the androgenic steroid hormone testosterone (T) as its end product. T is assumed to play a key role in human competitions and related behaviours (Zilioli & Bird, 2017). Moreover, it has been argued to partly mediate a trade-off between mating (attracting and competing for new mates) and parental effort (caring for offspring and one's partner; Muehlenbein & Bribiescas, 2005), in particular by increasing aggression and risk-taking at the expense of survival and nurturing behaviour (Muller, 2017). Due to sex differences in reproductive variance and intrasexual competition (as described above), T is assumed to be more relevant in men (Archer, 2009; Puts et al., 2015). In previous studies, the steroid hormone has been associated with dominance (meta-analytic r = .13, k = 13 samples, overall N = 2437; Archer, 2006), aggressiveness (meta-analytic r = .08, k = 42 samples, overall N = 9760; Archer, Graham-Kevan, & Davis, 2005) as well as competitiveness (N = 172 men; Eisenegger, Kumsta, Naef, Gromoll, & Heinrichs, 2017). One theory which describes the role of T in competitions is the *challenge hypothesis*, originally proposed for seasonally breeding birds (Wingfield, Hegner, Dufty, & Ball, 1990) and later applied to humans (Archer, 2006). It posits an acute rise in T in the face of various kinds of challenges, such as mating opportunities or intrasexual competition (for recent reviews, see Carré & Archer, 2017; Wingfield, 2017). Several studies have shown that men, after interacting with an (attractive) woman, had a larger T increase than after interacting with a male or waiting in a room alone (Roney, Lukaszewski, & Simmons, 2007; Roney, Mahler, & Maestripieri, 2003; van der Meij, Buunk, van de Sande, & Salvador, 2008). For instance, in the domain of contemporary sports competitions, a T increase in males has been shown in anticipation of, during and/or after engaging in sports such as soccer (N = 40; Edwards, Wetzel, & Winer, 2006), Japanese chess (N = 90; Hasegawa, Toda, & Morimoto, 2008) or wrestling (N = 15; Elias, 1981).

The *biosocial model of status* (Mazur, 1985, 2015; Mazur, Welker, & Peng, 2015) suggests the outcome of a competitive interaction to play a role regarding the exact strength (and direction) of T changes. It has been derived from research in male rhesus monkeys and predicts T increases after status gains, and declines in T after status losses. In humans, wins and losses in competitions have been shown to be linked with T increases and decreases, relatively. Although there is a wide range of moderating influences on whether and how winners show larger T increases than losers (e.g., home advantage; Fuxjager, Mast, Becker, & Marler, 2009; but see Fothergill, Wolfson, & Neave, 2017; ratio of opposite- versus same-sex individuals present; Miller, Manor, & McNulty, 2012), a recent meta-analysis (overall *N* > 2500) found a robust small effect size for the 'winner effect' (Geniole, Bird, Ruddick, & Carré, 2017).

An important qualification to the aspects mentioned above pertaining to T is the distinction between baseline levels (i.e., on a trait niveau, inter-individual differences) and acute fluctuations in T (i.e., reactivity, on an intra-individual state level). Notwithstanding large fluctuations in T levels throughout the day (diurnal variation with higher levels in the morning and a subsequent decline), yearly season and an individual's age (peaking at around 20-35 years in men), baseline T levels remain relatively low most of the time (Carré & Olmstead, 2015). However, as proposed by the challenge hypothesis, in the face of certain social interactions (like intrasexual competition or mate attraction), T levels increase rapidly (with associated physiological and behavioural effects as outlined above). Hence, given there seem to be benefits of elevated T levels (e.g., for mate attraction; Roney, Lukaszewski, & Simmons, 2007), one may wonder why do T levels return to baseline levels at all? Importantly, high T levels come at a cost, both behaviourally and physiologically. Behaviourally, increased T levels have been associated with reduced paternal care, increased energetic demands and risk-taking (Carré & Olmstead, 2015), which, in some contexts, may be detrimental for an individual's survival and evolutionary fitness. Physiologically, according to the *immunocompetence handicap hypothesis*, T acts as an immunosuppressant (Folstad & Karter, 1992). A recent meta-analysis showed medium-sized immunosuppressive effects of T (Foo, Nakagawa, Rhodes, & Simmons, 2017; although this may not be universally true across contexts; see Lorenz, Heiman, & Demas, 2017). Thus, to balance these benefits and costs, it appears a flexible and adaptive endocrinological system has evolved, with generally low baseline T levels and the potential for acute elevations in T in certain social contexts, such as intrasexual competition or mating opportunities.

For many of the above-mentioned associations, effects of T on behaviour and different outcome measures turned out to be rather weak (e.g., meta-analytic association between T and aggressiveness was pinpointed to be *r* = .08; Archer, Graham-Kevan, & Davis, 2005). It has been suggested that the HPG axis interacts with another endocrinological pathway, the hypothalamus pituitary adrenal (HPA) axis, with the glucocorticoid hormone cortisol (C) as its end product. Mehta and Josephs (2010) investigated the link between dominance and baseline T in two studies (study 1: *N* = 94 men and women; study 2: *N* = 57 men). Results revealed that associations between baseline T and dominance were moderated by participants' baseline C: A positive association became apparent only if C was low. When baseline C was relatively high, the relationships were non-significant (study 1) or even reversed (study 2). The authors coined this interaction between the HPG and HPA axes the *dual-hormone hypothesis* (Mehta & Josephs, 2010). In line with this, Popma and colleagues (2007) observed significant positive associations between baseline T and overt aggression in a sample of delinquent male adolescents only in those with low baseline C, but not when baseline C was high (*N* = 103). Following these two initial findings, effects of a TxC interaction have been shown on various kinds of behavioural tendencies and personality traits, which could be subsumed as status-seeking and -maintaining behaviours, as suggested by the dual-hormone hypothesis (e.g., on risk-taking: Mehta, Welker, Zilioli, & Carré, 2015; status-attainment: Sherman, Lerner, Josephs, Renshon, & Gross, 2016; reactive aggression: Geniole, Carré, & McCormick, 2011; see Mehta & Prasad, 2015 for a review). The exact neuroendocrinological mechanism of high baseline C attenuating effects of T on cognition and behaviour remains largely elusive. Some propositions which have been discussed are functional crosstalk between the HPG and HPA axes, inhibitory effects of C on the gonadal axis, neural mechanisms regarding threat responses (e.g., amygdala), reward sensitivity (e.g., ventral striatum), prefrontal-subcortical connectivity (e.g., involving the orbitofrontal cortex), and psychological processes such as approach and avoidance motivation (for more detail, see Mehta & Josephs, 2010;

Mehta & Prasad, 2015; Mehta, Welker, Zilioli & Carré, 2015). As multiple studies have already shown effects of a TxC interaction on behaviours and personality traits which are well implicated in competitive contexts (such as risk-taking, aggression, and status-attainment; for an overview, see Casto & Edwards, 2016), baseline C was included as a potential moderator in Manuscript 1.

Life history theory as a main theoretical framework

The above-mentioned findings and theories describe T as modulating trade-offs between mating and parenting (partly attenuated by high C), and can be theoretically embedded into life history theory, an important framework for explaining various kinds of human behaviours, especially in the realm of mating and reproduction (Stearns, 1992). According to life history theory, an individual faces different trade-offs of allocating resources (such as time and energy) to diverse kinds of tasks and the development of traits in the pursuit of maximizing evolutionary fitness (Del Giudice, Gangestad, & Kaplan, 2015). Zilioli and Bird (2017) have identified three evolutionarily relevant social contexts, in which such T-mediated trade-offs should be especially implicated: competitive interaction, exposure to potential mates, and interaction with offspring. One major trade-off is between mating (acquiring mates) and parental effort (nurturing offspring) behaviours, or, in other words, between competition and nurturance (van Anders, Goldey, & Kuo, 2011). High T is predominantly associated with behaviours related to mating (e.g., status acquisition) and low T with parenting (e.g., pair bonding), and ontogenetically T is closely linked with anabolic and androgenic effects (i.e., somatic growth and sexual differentiation, respectively; Zilioli & Bird, 2017). Beyond these more trait-like effects, associations between behaviours and T fluctuations on a state-level can also be understood in terms of life history trade-offs. Mating-related behaviours like intrasexual competition and interactions with potential partners should be linked with acute T elevations, in line with the challenge hypothesis, whereas parental effort, such as nurturing offspring or relationship maintenance, should be related to T decreases (though van Anders and colleagues argue that some aspects of parenting, such as offspring defense, may also be related to high T; van Anders, 2013; van Anders, Goldey, & Kuo, 2011). Similarly, C plays a role in modulating behaviours relevant from a life history perspective (e.g., fight/flight response, threat appraisal; Del Giudice, Gangestad, & Kaplan, 2015). Accordingly, a TxC interaction can be interpreted in light of life history theory. Status-seeking and competitive behaviours associated with T are attenuated by high C levels in times of high stress, thus decreasing reproductive effort (Del Giudice, Ellis, & Shirtcliff, 2011). Accordingly, the studies in this dissertation on men's competitive behaviour are embedded into life history theory as a main framework.

Outline Manuscript 1

Acute fluctuations in T have been suggested to be implicated in diverse kinds of challenges, including men's intrasexual competition (challenge hypothesis; Archer, 2006) and mating effort (e.g., female exposure studies; Roney, Lukaszewski, & Simmons, 2007). Some studies explored downstream effects of rapid T increases, such as behavioural changes. In their seminal work, Mehta and Josephs (2006) examined the effects of competition-induced T dynamics in males (*N* = 57), after having engaged in a rigged one-on-one competition, on the decision to compete again or engage in a cooperative task instead. T changes predicted the decision to compete again in losers, but not winners. The authors interpreted these findings as losers trying to regain status, modulated by changes in T. Carré, Putnam, and McCormick (2009) investigated associations between post-competition T fluctuations and aggressiveness in both males and females (*N* = 77). After performing a (same-sex) dyadic competition, participants' reactive aggressive behaviour was assessed with the *Point Subtraction Aggression Paradigm* (PSAP). While baseline T turned out to be unrelated to aggressiveness, T increases (from baseline T) predicted subsequent aggressive behaviour in male losers (and in male winners, moderated by self-reported trait dominance; for a review, see Carré & Archer, 2017). This is partly in line with Mehta and Joseph's finding (2006), underlining that especially losers are motivated to regain status, and that associations between T and behavioural changes are moderated by competition outcome. Carré, Baird-Rowe, and Hariri (2014) asked male and female participants (*N* = 83) to rate faces for trustworthiness, each before and after they had engaged in a competitive interaction (computer-based PSAP), and measured T reactivity. Trust ratings decreased significantly, *post* compared to *pre*, in men with higher T reactivity (but not women). The authors concluded that an acute T reactivity is linked with different aspects of subsequent social cognition and behaviour, such as trust. Finally, in an extensive review, Carré and Olmstead (2015) proposed competition-induced T fluctuations to modulate aggressive behaviour, competitive motivation and performance (including risk-taking; see also Vermeer, Riečanský, & Eisenegger, 2016), social cognition (e.g., trust, empathy, or moral decision-making) and mate-seeking behaviour (courtship displays). Thus, T reactivity may well be an evolved functional system, supporting competitive and mate-seeking behaviour across many contexts, especially in men.

Extant findings have been interpreted in such a way that T regulates cognition, behaviour and related physiological processes along a unidimensional dimension of either competition versus nurturance (van Anders, Goldey, & Kuo, 2011) or mating versus parental effort (Muehlenbein & Bribiescas, 2005; Muller, 2017). Relatedly, Roney (2016) has put forth a theoretical framework embedded into life history theory claiming a T-modulated trade-off between mating versus survival effort. These theoretical dimensions' endpoints largely overlap with the two main dimensions of another theoretical model of personality and social behaviour, the interpersonal circumplex model (Wiggins, 1982; Leary, 1957; see Figure 1), which has been shown to be widely relevant in human social behaviour (e.g., for a review on the role of the two main axes in social perception, see Fiske, Cuddy, & Glick, 2007). The interpersonal circumplex' two main axes, Dominance and Love, correspond to the dimensions of competition/mating and nurturance/parenting/survival, respectively. However, the circumplex model's main axes are defined as being orthogonal to each other, rather than unidimensional (as the T-mediated trade-offs outlined above). This provokes the question of how T-modulated changes in personality states are related to circumplex personality facets. Turan, Guo, Boggiano, and Bedgood (2014) investigated the association of salivary baseline T with circumplex personality traits (based on the Interpersonal Adjective Scales-Revised, IAS-R; *N* = 85 men). A positive correlation with agency/disconnectedness and a negative relationship with submissiveness/communion were found. Sellers, Mehl, and Josephs (2007) detected a positive, small-to-medium sized correlation of baseline T with self-reported dominance in both men and women

(*N* = 69). They argued, based on their additional finding of high temporal stability of baseline T levels (across five days), that T serves as a biological marker of inter-individual differences in dominance. However, it needs to be acknowledged that the meta-analysis by Archer (2006) found a smaller effect of baseline T on dominance (*r* = .13 from *k* = 13 samples, Sellers et al.: *r* = .25), hence the finding of Sellers and colleagues needs to be replicated. In the study by Eisenegger and colleagues (2017), a positive association between men's baseline T and competitiveness (choosing a competitive over a non-competitive payment scheme) was found. Thus, not only competition-induced fluctuations in T, but also baseline T levels seem to be related to behaviours and personality traits which could be summarized as competitive and status-seeking (Knight & Mehta, 2014), supporting humans, and especially men, in achieving and maintaining social status in competitive situations (Eisenegger, Haushofer, & Fehr, 2011).

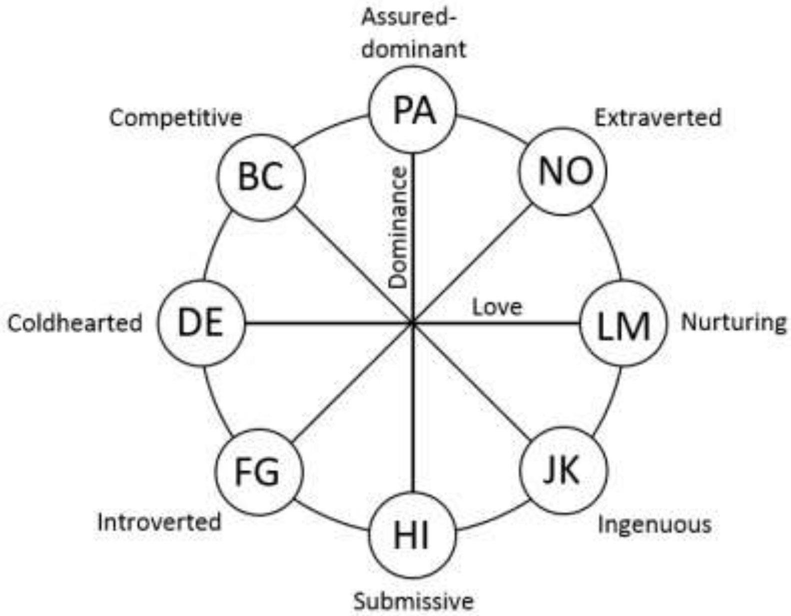

Figure 1. The interpersonal circumplex model with its eight personality facets and two main axes (adapted from Wiggins, Trapnell, & Phillips, 1988).

Although some studies, as mentioned above, pointed towards behavioural changes in association with T increases, there is a gap in the literature regarding how exactly personality states change in accordance with an acute T reactivity, when men engage in an intrasexually competitive situation. Previous studies have either focussed on a complete assessment of a range of personality traits (but no changes on a state level; Turan, Guo, Boggiano, & Bedgood, 2014), or on a narrow selection of personality and behaviour changes (e.g., competitiveness or aggressiveness; Carré, Putnam, & McCormick, 2009; Mehta & Josephs, 2006). Assessing a full range of personality facets, however, would deliver a more complete picture of which personality state facets exactly change in men engaging in an intrasexual competition, also in association with a potential hormonal reactivity. Buunk and Fisher (2009) showed that different personality facets are implicated in competitiveness. They developed a scale for capturing inter-individual differences in intrasexual competitiveness, and found correlations with neuroticism, agreeableness and extraversion (assessed with the NEO-FFI personality inventory; *N* = 258 males and females). Moreover, it has been suggested that behaviour and personality may be more strongly linked with state neuroendocrine function (such as T reactivity), hence on an intra-individual level, than with baseline measures (Carré & Olmstead, 2015). For example, Geniole, Carré, and McCormick (2011) found reactive aggressiveness (in the PSAP) to be associated with T and C reactivity, but not baseline measures, in men (*N* = 74). Accordingly, the studies in Manuscript 1 investigated associations between acute hormonal reactivity and a complete assessment of circumplex personality states. Using the circumplex model of personality with its two main axes Dominance and Love allows us to map personality states corresponding to the T-modulated trade-off between mating/competition and nurturance outlined earlier (Muehlenbein & Bribiescas, 2005; Muller, 2017; van Anders, Goldey, & Kuo, 2011).

Beyond associations of T with self-reported personality, T is related to men’s sexually dimorphic traits, such as muscularity (Frederick & Haselton, 2007), beardedness (Neave & Shields, 2008) and deep voices (Dabbs & Mallinger, 1999). Due to links with these traits, but also behavioural associations (such as aggressiveness or risk-taking; Geniole, Carré, & McCormick, 2011; Mehta, Welker, Zilioli, & Carré, 2015), T has been suggested to modulate male social signalling, both to male rivals and female potential mates, thus functioning in male sexual selection (Puts, 2010). Especially in intrasexually competitive and mating contexts, it is crucial for a rival or potential mate to perceive these signals accurately as cues to good condition (e.g., Sell, Cosmides, Tooby, Sznycer, von Rueden, & Gurven, 2009). However, there are only few studies on how such T-mediated behavioural changes are perceived by observers. Van der Meij and colleagues (2012) studied men's T reactivity in association with their behaviour during an interaction with a male or female confederate. Men interacting with a female, but not a male confederate, with a larger T reactivity were perceived by female observers as engaging in stronger self-presentation, as showing more interest in the confederate and more positive facial cues (*N* = 82). Similarly, Roney, Mahler, and Maestripieri (2003) found men's T reactivity after interacting with a female confederate to be positively correlated with the confederate's rating of how much the males tried to impress her (*N* = 37; see also Slatcher, Mehta, & Josephs, 2011). Thus, while extant studies have focussed on a specific aspect of men's behaviour in relation to T levels (e.g., mating behaviour), there is a gap in the literature regarding associations between acute T fluctuations and a complete assessment of observer-perceived personality states. Beyond employing the interpersonal circumplex model, we created specific items directly capturing observer perceptions in opposite behavioural domains associated with T (competition vs. nurturance; van Anders, Goldey, & Kuo, 2011). Three dimensions were used to tap upon men's T-mediated social signalling: self-displaying and self-assurance (both related to agency and competition), and cooperativeness (mapping nurturance). These judgments were performed by male and female observers based on short video-recordings of the target men both before (*pre*; calm state and baseline T) and after (*post*; aroused state and presumably reactive T) engaging in a dyadic competitive interaction (see Ambady & Rosenthal, 1992, for evidence that personality can be assessed in an accurate way from observations as short as 30 secs). Hence, the first Manuscript investigated both self-reported and observer-rated personality state changes in relation to competition-induced T fluctuations in men.

A further important feature of our first Manuscript is that participants' T reactivity was naturally induced (by means of a dyadic competition and female exposure), in contrast to earlier studies using exogenous T (e.g., gel; Welling, Moreau, Bird, Hansen, & Carré, 2016). This renders our findings more generalizable, since in T administration studies only the exogenous influence in an artificial (likely laboratory) setting was tested. Our findings regarding associations with T reactivity have higher ecological validity, as it emerged naturally (but still in a laboratory setting) and we measured both baseline T before and *post* levels after the competition, which means we assessed the actual magnitude of change (in contrast to most T administration studies, where only the amount of T administered is known). In addition, the outcome of our dyadic competition emerged naturally, unlike some previous studies, which used rigged outcomes (e.g., Geniole, Busseri, & McCormick, 2013). Our design should be more credible for participants and yield more valid associations between hormonal and personality changes, potentially moderated by competition outcome (e.g., Mehta & Joseph, 2006).

The first Manuscript's studies were specifically designed to address the question of how acute hormonal changes (T, also in interaction with baseline C) are intertwined with personality state changes in men in an intrasexual competition, constituting an evolutionarily salient social context (Zilioli & Bird, 2017). This yields insights into the role of acute fluctuations in steroid hormones and personality in men's intrasexually competitive behaviour. It extends our knowledge on an important evolved functional system (i.e., neuroendocrine reactivity) crucially implicated in men's social interactions and signalling, supporting their status-seeking, mate acquisition and eventually reproductive success. Hence, two key questions in sexual selection were being addressed, namely, inter-individual differences and intra-individual associations (between hormonal and personality changes) in men in a mating-related situation, and how these are perceived by observers in terms of social signalling (Miller, 2000).

Outline Manuscript 2

Whereas Manuscript 1 investigated hormonal reactivity and personality state changes in men engaging in an intrasexually competitive situation, Manuscript 2 examined the contribution of intrasexual competition and associated traits to men's mating success (as a proxy of reproductive success), relative to female mate choice (and traits related to men's sexual attractiveness), as mechanisms of sexual selection. One indicator for traits having been under sexual selection is that they are sexually dimorphic (i.e., traits which show consistent sex differences between males and females; Hill, Bailey, & Puts, 2017). The development of these sexually dimorphic traits, such as body height or voice pitch, is modulated by androgenic hormones (perinatal and pubertal T levels, for instance; Puts, 2010; Puts, Jones, & DeBruine, 2012). Hence, in Manuscript 2 the characteristics under scrutiny are assumed to be related to hormonal variables on a trait level and ontogenetically, whereas in Manuscript 1 the association is state-like and on a proximate level. Besides sexual dimorphism, a further indicator for a trait being or having been influenced by sexual selection is that its phenotypic variation is linked with mating success (which may translate into actual reproductive success; Puts, Bailey, & Reno, 2015). Finally, because such traits are especially advantageous after sexual maturation (when individuals become active on the mating market) and often costly to develop and maintain (for example, in line with the immunocompetence hypothesis; Folstad & Karter, 1992), they may have evolved to develop and/or increase in their expression around puberty (Hill, Bailey, & Puts, 2017). The focus in this Manuscript is on sexually dimorphic traits related to men’s physical dominance (which could be functional in male-male competition) and sexual attractiveness (implicated in attracting female mates). Besides male-male competition and female mate choice, there are further mechanisms of sexual selection, such as scrambles, sexual coercion, and sperm competition (Puts, 2016). These mechanisms have played some role in the evolution of men’s traits; however, male contest competition and female mate choice likely have been the most influential ones, so that we focussed on these, in line with previous studies (e.g., Hill et al., 2013; Puts et al., 2016). Thus, Manuscript 2 addresses a further key question in sexual selection: how are men’s traits related to (a proxy measure of) their overall fitness (Miller, 2000)?

A range of men’s putative sexually selected traits has already been associated with elevated mating success (number of copulatory partners, age at first sexual intercourse) and/or reproductive success in earlier research, such as muscularity and physical prowess, body height, facial and vocal masculinity (for an overview, see Hill et al., 2013 and Puts, Bailey, & Reno, 2015). Recent theorizing suggests that these traits, which could be subsumed under the realm of physical dominance, evolved especially due to their functioning in male-male contests (whether for signalling strength and formidability, or in actual fighting; Hill, Bailey, & Puts, 2017; Puts, Bailey, & Reno, 2015), even though previously it had been assumed that female mate choice is the main mediator in the evolution of male sexually dimorphic traits (Puts, 2010). In the last few years, evidence accumulated that male-male competition might have played a stronger role in sexual selection, compared to female mate choice. Hill and colleagues (2013) investigated the influence of female mate choice (framed as sexual attractiveness) and male-male competition (operationalized as physical dominance) and related traits on mating success (*N* = 63 men). Objectively measured traits (facial and vocal masculinity, body height and girth - a composite measure consisting of upper arm, chest and shoulder girth, and body weight) as well as sexual attractiveness and physical dominance (reported by familiar female and male acquaintances, respectively) were assessed in relation to the number of sexual partners in the previous year. Physical dominance and associated traits (in particular, girth and vocal masculinity), but not sexual attractiveness, significantly and positively predicted mating success. In a further study on men's vocal characteristics (*N* = 175), highly sexually dimorphic voice pitch (the perceptual correlate of fundamental frequency), was more strongly negatively related to male-rated dominance than to female-rated attractiveness (Puts et al., 2016). These findings imply a larger influence of contest competition than female mate choice in the evolution of males' sexually dimorphic traits. Similarly, Saxton, Mackey, McCarty, and Neave (2016) found positive linear effects of masculine (lower) voice pitch and beard growth on perceptions of dominance based on video recordings (*N* = 6 men, overall 96 stimuli videos with different beard growth stages and voice pitch manipulations). For perceived attractiveness, only a negative curvilinear relationship with voice pitch emerged (i.e., intermediate values were most attractive). The authors interpret these findings as suggesting context-dependent (intra- or intersexual selection), differential optimum levels of facial hair and voice pitch (e.g., low and intermediate voice pitches are most dominant and attractive, respectively). Antfolk and colleagues (2015) provide evidence for a role of female mate choice, in that men's sexual activity appeared to be more constrained by women than vice versa. However, because no measure of male-male competition was included, the relative influence of these two mechanisms of sexual selection could not be ascertained from their study. Overall, these studies on the relative contributions of male-male competition and female mate choice to men's mating success point towards a somewhat stronger influence of the former on sexual selection, contrary to earlier theorizing (Puts, 2010).

In contrast, other relevant studies investigated only one of the two primary mechanisms of sexual selection (male-male competition or female mate choice) at a time (Hunt, Breuker, Sadowski, & Moore, 2009), not allowing any conclusion on the relative influences of these two mechanisms. Consequently, Hunt and colleagues recommended to examine both mechanisms simultaneously, because relevant facial, vocal, and bodily traits may be developmentally correlated (e.g., Feinberg, 2008). For a full account of sexual selection, these two mechanisms' interaction (i.e., correlational selection) needs to be analysed, as the relative influences of male-male competition and female mate choice can strengthen or attenuate each other, and differ across time and contexts (Hunt et al., 2009). In addition, selection is not always linear, and optimum levels of traits are not necessarily on a distribution's endpoints, so that effects are better described by quadratic functions. For example, in one study (Cunningham & Barbee, 1990) curvilinear effects of facial masculinity (N = 60 male stimuli) on female perceptions of attractiveness (N = 100 raters) were shown, with most favourable ratings for moderate masculinity characteristics. In a review of associations between male body height and reproductive success, Stulp and colleagues (2012) reported a mixture of positive, negative, curvilinear, and null effects (k = 19 samples). Hence, our second Manuscript analysed nonlinear (besides linear) effects of male-male competition, female mate choice, and associated traits on mating success, contributing to a complete understanding of how sexually dimorphic traits evolved in men (Hunt et al., 2009).

Prior studies on sexual selection showed further limitations. First, sample sizes were rather small (e.g., only N = 63 men in Hill et al., 2013), limiting the robustness of these findings. Secondly, the samples in Hill and colleagues and Puts and colleagues had very low mean ages and narrow age ranges around 20 years, further questioning the robustness and generalizability of these findings.

Consequently, these findings need to be replicated, especially in light of the current replication crisis in psychology and related fields (see below; Open Science Collaboration, 2015). Thirdly, so far, only a limited selection of men’s sexually dimorphic traits has been investigated regarding their association with mating and/or reproductive success, such as vocal (Puts et al., 2016), facial and bodily characteristics (Hill et al., 2013). Additional traits, which may be or have been under sexual selection have been ignored so far. For example, an influential trait in male-male competition is physical strength (Sell, Hone, & Pound, 2012), increasing perceptions of physical dominance (which might augment mating success; Hill et al., 2013). As discussed above, the steroid androgen T has been proposed to contribute to mechanisms facilitating trade-offs between mating and parenting efforts and social signalling in competition, especially in men (e.g., Muller, 2017; Puts et al., 2015), and has been associated with perceived attractiveness (e.g., Roney et al., 2006; *N* = 39 men), dominance (e.g., Dabbs, 1997; *N* = 119 men) and mating success (Peters, Simmons, & Rhodes, 2008; *N* = 119 men; but see Puts et al., 2015). Moreover, sexually dimorphic traits, including physical strength, are assumed to be developmentally linked with T, and therefore it would be interesting to investigate direct effects of men’s current baseline T levels and physical strength on their mating success. Hence, this study investigated whether baseline T levels and other sexually dimorphic traits primarily function as social signals to same-sex rivals (in male-male competition) or opposite-sex potential partners (in female mate choice), and through which mechanism they subsequently affect mating success.

Because most studies on sexual selection in humans have employed a cross-sectional design (e.g., Hill et al., 2013), assessing men’s traits and their mating and/or reproductive success at the same time point, it is difficult to conclude whether the investigated traits actually had causal influence on mating/reproductive success. Alternatively, a third variable not assessed in the study could have caused variation in both trait and mating/reproductive success measures. To establish temporal precedence, one crucial component of causality, we employed a longitudinal design in our study in Manuscript 2. Eighteen months after the initial data collection (measuring participants’ traits, amongst others), participants were invited to report their mating success in an online questionnaire. Thus, this study provides some evidence on causal influence of men's sexually dimorphic traits on their mating success during the following 18 months. To investigate the relative influences of female mate choice and male-male competition on sexual selection in men, potentially mediating effects of sexual attractiveness and physical dominance were also examined.

Wrapping up the introduction

In this dissertation, I envisaged to investigate various aspects of male competition, mainly in the realms of sexual selection and life history theory. Individual differences both on a state and trait level were examined. Manuscript 1 focused on proximate mechanisms of competitive behaviour, acute personality and hormonal changes in an intrasexually competitive mating situation. Findings regarding the roles of hormone reactivity and personality state change were interpreted under the realm of life history theory (Del Giudice, Gangestad, & Kaplan, 2015; Stearns, 1992): what are the effects of acute fluctuations in T on self-reported and observer-perceived personality state changes? Men's phenotypic plasticity, also in terms of T-mediated social signalling, in an evolutionary salient social context was investigated (Puts, 2010, 2016). In Manuscript 2, we focussed on men's sexually dimorphic traits implicated in such contest competitions and mate acquisition. A more functional approach was assumed by assessing the prediction of men's mating success by various traits related to physical dominance and sexual attractiveness. Hence, effects of T-modulated social signalling, in terms of observer-perceptions of dominance and attractiveness, on mating success was investigated as well. This likely expands knowledge on the relative role of the two primary mechanisms of sexual selection, male-male competition versus female mate choice, in the evolution of men's sexually dimorphic traits.

Both Manuscripts investigated individual differences in men's sexually dimorphic characteristics (Manuscript 1 on a state, and Manuscript 2 on a trait level), including effects of the steroid androgen hormone T, in intrasexually competitive contexts. Manuscript 1 was situated in a direct, dyadic male contest (including the presence of an attractive female), whereas Manuscript 2 involved male-male competitive ability (observer-judged physical dominance) as a potential mediator of associations between sexually dimorphic traits and mating success. The present studies provided further insights into different levels of analysis of competitive behaviour. According to Tinbergen (1963), a study of human behaviour is only complete when taking into account four perspectives (proximate, functional, phylogenetic, and ontogenetic mechanisms). The first Manuscript adopted a proximate perspective by investigating the role of acute hormone fluctuations in synergy with personality state changes in an immediate competitive situation, whereas Manuscript 2 added evidence on both functional (men's mating success predicted by their sexually dimorphic traits) and phylogenetic mechanisms (relative contribution of male-male competition and female mate choice to the evolution of men's traits). Since competition is ubiquitous in humans throughout human evolution, we studied important aspects of human behaviour and their evolution in this crucial kind of social setting, under theoretical umbrellas of life history theory (Del Giudice, Gangestad, & Kaplan, 2015; Stearns, 1992) and sexual selection (Darwin, 1871; Fisher, 1930).

Open science

Recently, the credibility of psychological science was questioned, after a large number of research teams throughout the world had set out to replicate published findings in different projects, such as the *Reproducibility Project* (Open Science Collaboration, 2015) or the *Many Labs* projects (Ebersole et al., 2016; Klein et al., 2014, 2015). Somewhat surprisingly to most collaborators involved and the whole community of psychological researchers, only between approximately one fifth and two thirds of these replications showed a positive result (i.e., statistically significant and in the originally hypothesized direction), meaning that the remaining roughly 33-80 % of findings could not be repeated. For example, only 23 % of studies (7/31) in the prestigious *Journal of Personality and Social Psychology* could be replicated successfully. This discrepancy has been attributed to publication bias (file-drawer effect, referring to a higher likelihood of publishing positive findings, compared to null results or those in opposite direction to previous hypothesizing), low statistical power (mainly due to small samples) and questionable research practices (QRPs) like "*p*-hacking" (analysing data and interpreting results until a certain level of statistical significance is beaten) and "harking" (hypothesizing after results are known). To increase the robustness and reliability, and hence the reproducibility, of psychological research, several strategies have been proposed. These include, but are not limited to, precisely formulating a study’s methods and hypotheses before (and of course sticking to these during) data collection, in so-called preregistrations, or increasing transparency and the ease of replicating a study by uploading data and materials with published articles (Munafo et al., 2017). In line with these suggestions, the methods and hypotheses of Manuscript 1 were preregistered on the Open Science Framework (see links in the manuscript below). Moreover, the data and material (analysis scripts) for both Manuscripts 1 and 2 were made available online (links in the manuscripts). These should serve the purpose of reducing researcher degrees of freedom (including *p*-hacking and harking). In addition, these two Manuscripts contribute to a robust science by replicating previous findings, albeit in an extended way. Manuscript 1 attempted to reproduce previous findings on acute T increases in the face of a competitive challenge and female exposure (e.g., Archer, 2006; Roney, Mahler, & Maestripieri, 2003), and Manuscript 2 put previous results to the test of a stronger role of men’s dominance and related traits, compared to attractiveness, in sexual selection (e.g., Hill et al., 2013; Puts et al., 2016). Thus, findings from this dissertation project add to a reliable, efficient and transparent psychological science by endorsing principles of an open and robust science, such as employing relatively large samples (resulting in a high statistical power), robust analyses, partly preregistered methods and hypotheses, as well as open data and materials (e.g., Munafo et al., 2017).

3. Manuscript 1

Effects of male testosterone and its interaction with cortisol on self- and observer-rated personality states in a competitive mating context

Effects of male testosterone and its interaction with cortisol on self- and observer-rated personality states in a competitive mating context

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Abstract

Increases in human male testosterone (T) levels have been found after intrasexual competitions and exposure to females, facilitating competitive and courtship behaviours. This suggests that T reactivity should affect relevant personality state changes that are also observable to others. How exactly T reactivity, also under potential buffering effects of Cortisol (C), relates to personality state changes is unclear. In a preregistered study, we aimed at inducing T increases in young men (*N*=165) through dyadic intrasexual competitions while exposed to a female experimenter. We investigated self-reported and video-based observer-rated personality state changes, as captured by the Interpersonal Circumplex and social impressions, in relation to hormonal levels. Results revealed increases in self-reported competitiveness, as well as observer-rated dominance and self-assurance, relative to a control group and moderated by T reactivity and partly by TxC interactions. Thus, male T reactivity in a competitive mating context increased competitiveness/dominance, but did not decrease nurturance. This provides further insights into how hormonal and personality responses to challenges are intertwined in men, and partly supports a role of T in mediating a life history trade-off between mating/competing and parenting, as well as signalling dominance to rivals and potential mates.

Keywords testosterone, cortisol, male competition, female exposure, interpersonal circumplex

Introduction

Humans compete for access to mates and social status in order to reproduce and eventually reach higher biological fitness (Puts, 2016). A wide range of fine-grained mechanisms have evolved over human evolutionary history to support pursuing these goals. One important mechanism implicated here is the endocrinological system. Hormones act as physiological coordinators, influencing several organs and processes simultaneously, including human perception and behavioural dispositions (Roney, 2016). The steroid hormone testosterone (T) plays a key role in human competitive behaviour. It has been shown to partly mediate a trade-off between mating and parenting effort (Muehlenbein & Bribiescas, 2005), in particular by increasing aggression and risk-taking at the expense of survival and nurturing behaviour (Muller, 2017). T has further been suggested to modulate social signalling in intrasexual (dominance contests) and intersexual (mate attraction) contexts (Puts, 2010). T levels are related to relationship status and parenthood, in that lower T has been found in partnered, compared to single individuals (van Anders & Watson, 2006), and in fathers relative to non-fathers (Gettler, McDade, Feranil, & Kuzawa, 2011). T is particularly relevant in men compared to women, presumably due to different trade-offs concerning reproductive strategies and hence intrasexual competition being more prevalent (Archer, 2009; Puts et al., 2015). If T responses to competitive and mating-related situations adaptively trigger relevant behavioural tendencies and social signals, they should mediate changes in corresponding personality states, which should also be accurately detectable by observers. In the present preregistered study, we seek to clarify the role of T and its effects on personality states in an intrasexually competitive situation among men.

Challenge hypothesis and female exposure studies

According to the challenge hypothesis, which was originally proposed for seasonally breeding birds (Wingfield, Hegner, Dufty, & Ball, 1990) and later applied to humans (Archer 2006), there is an acute increase in T levels in the face of various kinds of challenges, such as mating opportunities or intrasexual competition (for recent discussions, see Carre & Archer, 2017; Wingfield, 2017). The challenge hypothesis stems from the field of behavioural ecology, where acute changes (such a T reactivity) are termed plasticity (Dingemanse, Kazem, Reale, & Wright, 2010) and correspond to state changes in personality psychology. One contemporary domain where such T reactivity becomes apparent in humans is sports competitions. A T increase in male competitors has been shown in anticipation of, during and/or after engaging in sports competitions such as soccer (*N* = 40; Edwards, Wetzel, & Winer, 2006), Japanese chess (*N* = 90; Hasegawa, Toda, & Morimoto, 2008) or wrestling (*N* = 15; Elias, 1981). In some studies, T reactivity was shown to be higher in winners compared to losers of sports competitions, which has been termed the "winner effect". Although there is a mixture of positive and negative findings, a recent meta-analysis found overall evidence for larger T increases in winners relative to losers (*k* = 60 effect sizes, overall *N* > 2500 men and women; Geniole, Bird, Ruddick, & Carré, 2017).

Another setting where rapid increases in men's T levels have been shown are mating opportunities, or so-called "female exposures". A range of studies have shown that a simple interaction with an attractive woman as short as five minutes can suffice to raise T in men (free T usually measured from saliva; Fiers et al., 2014). For example, Roney, Mahler and Maestripieri (2003) showed a significant increase in T in men (*N* = 37) after engaging in a short conversation with a young woman. No increase was detected in a control condition, in which the participants interacted with a male experimenter. In a similar study (van der Meij, Buunk, van de Sande, & Salvador, 2008), a T increase was found in men (*N* = 30) after interacting with a female confederate, and T reactivity was stronger in those men with a more aggressively dominant personality. Thus, it seems, short informal interactions with opposite-sex members are sufficient to reliably elicit a T response, at least in men (see also Roney, Lukaszewski, & Simmons, 2007; van der Meij, Almela, Buunk, Fawcett, & Salvador, 2012). Importantly, these T increases in response to mating opportunities and competitive interactions, as suggested by the challenge hypothesis, are assumed to be mediated or moderated by both individual differences (personality and cognitive variables such as aggressive dominance, one's involvement and perceived control; Casto & Edwards, 2016a; Salvador, 2005) and situational characteristics (termed "contextual factors", e.g., one's opponent's self-efficacy; van der Meij, Buunk, Almela, & Salvador, 2010). One particularly important contextual factor, the outcome of a competition, can be more generally framed as status gains or losses, which have been linked to T levels in the biosocial model of status (Mazur 1985, 2015; Mazur, Welker, & Peng, 2015). This model has been derived from research in male rhesus monkeys and predicts T increases after status gains and declines in T after status losses, such as in competitive interactions, as mentioned above. Thus, the evidence reviewed so far shows that not only does T fluctuate in anticipation of, during and after competitions in humans, but also in accordance with variations in contextual factors such as rank, relationship status or parenthood.

Testosterone and personality

Extant findings have been interpreted in such a way that T regulates cognition, behaviour and related physiological processes along a unidimensional competition versus nurturance dimension (steroid/peptide theory of social bonds; van Anders, Goldey, & Kuo, 2011), a mating versus parenting dimension (Muller, 2017), or, as a theoretical framework embedded into life history theory, a trade-off between mating versus survival effort (Roney, 2016). These theoretical dimensions' endpoints largely overlap with the two main dimensions of another theoretical model of personality and social behaviour, the interpersonal circumplex model (Wiggins, 1982; Leary, 1957; Figure 1), which has been shown to be widely relevant in human social behaviour (e.g., for a review on the role of the two main axes in social perception, see Fiske, Cuddy, & Glick, 2007). The interpersonal circumplex' two main axes, Dominance and Love, correspond to the dimensions of competition/mating and nurturance/parenting/survival, respectively. However, the circumplex model's main axes are defined as being orthogonal to each other, rather than unidimensional (as the T-mediated trade-offs outlined above). This provokes the question of how T-modulated changes in personality states are related to circumplex personality facets. Turan, Guo, Boggiano, and Bedgood (2014) investigated the association of baseline T with the interpersonal circumplex personality traits (based on the Interpersonal Adjective Scales-Revised, IAS-R; *N* = 85 men). A positive correlation with agency/disconnectedness (facet BC) and a negative relationship with submissiveness/communion (facet JK) was found. In addition, Sellers, Mehl, and Josephs (2007) found positive, small-to-medium sized correlations of baseline T with self-rated dominance (r = .25; corresponding to the circumplex model's main axis Dominance) in both men and women (N = 69). They argue, also based on their additional finding of high temporal stability of T levels (across five days), that T may well serve as a biological marker of inter-individual differences in dominance. However, it needs to be acknowledged that a meta-analysis found a somewhat smaller effect of baseline T on dominance (conceptualized as over-ranking oneself; k = 13 samples, overall N = 2437; weighted r = .13; Archer, 2006), hence the finding of Sellers and colleagues (2007) needs to be replicated. Thus, some first findings, mostly from small samples, indicate baseline T may be related to self-perceptions of dominance, and negatively to submissiveness (both facets forming the circumplex model's vertical main axis; Figure 1) on a trait level, corresponding to the life history trade-off between parenting and mating (Muehlenbein & Bribiescas, 2005; Muller, 2017; Zilioli & Bird, 2017).

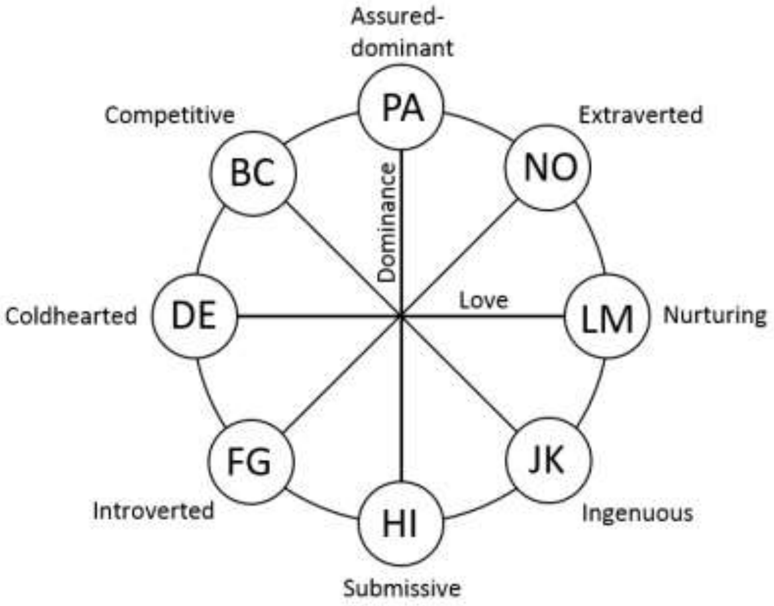

Figure 1. The interpersonal circumplex model with its eight personality facets (adapted from Wiggins, Trapnell, & Phillips, 1988).

Testosterone and intra-individual differences

Many of the inter-individual associations between T and behaviour in the literature appear to be rather weak. For example, regarding baseline T and aggression in humans, a meta-analysis by

Archer, Graham-Kevan, and Davis (2005; update of an earlier meta-analysis by Book, Starzyk, & Quinsey, 2001) pinpointed the average correlation to be *r* = .08 (weighted by sample size; *k* = 42 samples; overall *N* = 9760). Somewhat larger, but still small, overall associations have been found between baseline T and dominance (see above; Archer, 2006). Two arguments have been put forth regarding why these links with T levels might be rather weak, and how a higher amount of variance in these behaviours and personality traits could be explained. Firstly, it has been proposed that individual differences in these behaviours and traits may be more reliably related to acute fluctuations in T than to baseline T, hence on an intra- rather than an inter-individual level (Carré & Olmstead, 2015). Across three studies (total *N* = 224 men), antagonistic behaviour during a competitive interaction (Point Subtraction Aggression Paradigm, PSAP) was associated positively with T reactivity, but not baseline T, in men (Carré, Putnam, & McCormick, 2009; Geniole, Carré, & McCormick, 2011; Geniole, Busseri, & McCormick, 2013). In another study (Carré, Baird-Rowe, & Hariri, 2014), men's (*n* = 42, but not women's, *n* = 41) decreased trust ratings of emotionally neutral faces were predicted by their T increases, but not baseline T, after having engaged in the PSAP. In one of the first studies on the effects of competition-induced T dynamics on behaviour, Mehta and Josephs (2006) examined T changes in males (*N* = 57) after having engaged in a rigged one-on-one competition. T changes predicted the motivation to compete again, rather than doing a cooperative task after the initial competition, in losers, but not winners. The authors interpreted the findings as losers trying to regain status (after a loss), which is mediated by changes in T. In a similar study (Carré, Putnam, & McCormick, 2009), both male and female participants performed a (same-sex) dyadic competition (*N* = 77). Afterwards, the PSAP was employed to measure reactive aggressive behaviour. While baseline T turned out to be unrelated to aggressiveness, T increases (from baseline T) predicted subsequent aggressive behaviour in male, but not female, losers. Additionally, the interaction of T increases and trait dominance was related to aggressiveness in male winners only (see also Carre & Archer, 2018 for a review). Eisenegger and colleagues (2017) had men (*N* = 172) engage in a mathematical skills-based task, and found positive associations between baseline T and competitiveness (choosing a competitive over a non-competitive payment scheme), as well as between T reactivity during the competition and confidence in one's own performance. Finally, in an extensive review, Carré & Olmstead (2015) proposed competition-induced T fluctuations to be modulating aggressive behaviour, competitive motivation and performance, social cognition (e.g., trust, empathy, or moral decision-making) and mate-seeking behaviour (courtship displays), as well as increasing risk-taking (see Carré, Ruddick, Moreau, & Bird, 2017 for a review; Vermeer, Riečanský, & Eisenegger, 2016). Thus, behaviours and personality traits relevant in an intrasexually competitive context may well show stronger links with acute T fluctuations than with baseline levels, which will be investigated further in this study. However, the question remains how state changes along interpersonal circumplex personality facets are associated with acute T increases in an intrasexually competitive context.

The dual-hormone hypothesis

As a second explanation for weak links of T with behaviour and personality, an endocrinological interaction has been proposed. Mehta and Josephs (2010) examined associations between observer-rated trait dominance and baseline T in two studies (study 1: *N* = 94 men and women; study 2: *N* = 57 men). They found that effects depended on the levels of another hormone, the glucocorticoid cortisol (C). In particular, a positive association between T and dominance became apparent only if baseline C was low (for men and women together in study 1, non-significant if analyzed separately). When baseline C was relatively high, the associations were non-significant (study 1) or even partly reversed (study 2). The authors suggested the interaction of two neuroendocrine axes, the hypothalamus pituitary gonadal (HPG) and hypothalamus pituitary adrenal (HPA) axes, to be at work in regulating dominance, and coined this the dual-hormone hypothesis (Mehta & Josephs, 2010; see also Popma et al., 2007). Since then, a range of studies has examined associations with various kinds of behavioural tendencies and personality traits, which could be subsumed as status-seeking and -maintaining behaviours, and found support for the dual-hormone hypothesis (e.g., on risk-taking: Mehta, Welker, Zilioli, & Carré, 2015; status-attainment: Sherman, Lerner, Josephs, Renshon, & Gross, 2016; reactive aggression: Geniole, Carré, & McCormick, 2011; see Mehta & Prasad, 2015 for a review). Since multiple studies have already shown effects of an interaction between T and C in a fairly consistent way, it seems warranted to include baseline C as a potential moderator in our study.

Testosterone and observer perceptions

So far, a range of associations of T with people's behavioural propensities and self-reported personality traits have been reviewed. Beyond these, T has been suggested to be related to men's secondary sexual traits, and hence to modulate social signalling to both same-sex (e.g., threatening rivals) and opposite-sex (attracting potential mates) members (Puts, 2010). Examples of traits and behaviours which are ontogenetically or proximately linked to T and play a role in social signalling include men's muscularity (Frederick & Haselton, 2007), risk-taking (Mehta, Welker, Zilioli, & Carré, 2015) and mating behaviour (van der Meij, Almela, Buunk, Fawcett, & Salvador, 2012; see also Andersson, 1994). In intrasexually competitive and mating contexts, it is crucial for both rivals and potential mates to perceive these signals accurately as cues to good condition (Sell, Cosmides, Tooby, Sznycer, von Rueden, & Gurven, 2009). However, there are only few studies on whether and to what extent such T-mediated behavioural changes (in line with the challenge hypothesis) are perceived by rivals and potential mates. Van der Meij and colleagues (2012) studied men's T reactivity in association with their behaviour during an interaction with a male and female confederate. After interacting with a female, but not a male confederate, men with larger T reactivity were perceived by female observers as engaging in stronger self-presentation, and as showing more interest in the confederate and more positive facial cues (*N* = 82). These results are similar to Roney and colleagues' study (2003), in which men's T reactivity after interacting with a female confederate was positively correlated with the confederate's rating of how much the males tried to impress her. Slatcher, Mehta, and Josephs (2011) had men (*N* = 76) engage in a mate competition for the attention of an attractive female confederate against another male participant. For those high in self-reported dominance, a positive association of baseline T with their observable dominant behaviour during the mate competition, as judged from video recordings, and a negative link with their opponent's observable dominant behaviour were found. While the extant studies have focussed on a specific aspect of men's behaviour in relation to T levels, there is a gap in the literature regarding associations between acute T fluctuations and a more comprehensive assessment of observer-perceived personality states.

This study: Aims and hypotheses

The current study aims to replicate and further investigate the reactivity of T in men in response to exposure to a potential mate and an intrasexually competitive situation (in line with the challenge hypothesis; Archer, 2006). In particular, pairs of men were asked to engage in a dyadic competition (mixture of four cognitive and physical disciplines), while being supervised by an attractive female confederate. Before (*pre*) and after (*post*) the competition, saliva samples were taken to assess baseline T and T reactivity, as well as baseline C. Men completed a state version of an interpersonal circumplex personality questionnaire. In order to capture behavioural changes and observer-perceptions of these, our male participants were video-recorded both before (in a calm state, with baseline T levels) and after (in an aroused state, purportedly with elevated T) engaging in a dyadic male competition. In particular, participants were asked to present themselves describing their personal strengths within a short time frame (1 min.), thus engaging a somewhat challenging task (Study 1). Male and female observers subsequently judged these video recordings for personality states (also using the interpersonal circumplex; Study 2) and self-created “social impression” items (Study 3). We created items within three domains, which we believe are especially relevant in the context of both intrasexual competition and female mate choice. The domain “cooperativeness” should correspond to the interpersonal circumplex model’s Love main axis (e.g., Wiggins, 1982; see also the findings of van der Meij et al., 2012 on T reactivity and affiliative behaviour), “self-display” should tap into behaviour signalling to both male rivals and female potential mates (e.g., Roney, Lukaszewski, & Simmson, 2007) and “self-assurance” should capture perceptions of a man’s strength and confidence. These three domains are supposed to directly map onto the T-mediated trade-off between mating/competition (self-display and self-assurance) and parenting/nurturance (cooperativeness; Muehlenbein & Bribiescas, 2005; Muller, 2017; Roney, 2016; van Anders, Goldey, & Kuo, 2011). Previous research has shown that personality traits can be reliably inferred by observers after viewing short recordings of behaviour, which are referred to as “thin slices of behaviour” (Ambady & Rosenthal, 1992; Borkenau, Mauer, Riemann, Spinath, & Angleitner, 2004). We hence tested influences of T changes on both self-reported and observer-rated personality states, including observer-perceptions of social impressions relevant in men’s signalling behaviour (e.g., Puts, 2010). Furthermore, we examined the interaction of baseline C with T reactivity in association with personality state changes (according to the dual-hormone hypothesis; Mehta & Josephs, 2010). For robustness checks, analyses in Study 1 were additionally performed including the following preregistered control variables, which have been associated with T before: participants’s age, BMI, relationship status, recent sexual experience, self-reported positive/negative affect, stress, and self-esteem (Keevil et al., 2017; Roney, Mahler, & Maestripieri, 2003; Schultheiss & Stanton, 2009; van Anders & Watson, 2006; van der Meij, Buunk, van de Sande, & Salvador, 2008; Vermeulen, Goemaere, & Kaufman, 1999). Analyses in Studies 2 and 3 were re-run including the preregistered control variables participant age, relationship status and sexual identity (in Study 3a only the former two; Keevil et al., 2017; van Anders & Watson, 2006). The methods and hypotheses of all three studies were preregistered on the Open Science Framework (Study 1: osf.io/8n7ev; 2a: osf.io/rp4qk; 3a: osf.io/76bwj; 2b and 3b: osf.io/uhzf3). Specifically, the following hypotheses were tested:

1. Salivary T increases relative to baseline in male participants after a dyadic intrasexual competition under female exposure in the experimental group, but not in a control group in which participants do not compete and are supervised by a male experimenter the whole time.
2. a) We hypothesize larger *pre-post* changes (before to after the competitive interaction) in the experimental than in the control group in the following self-reported personality states along the interpersonal circumplex (which are assumed to be implicated in a competitive mating situation; Roney, 2016; van Anders, Goldey, & Kuo, 2011): increases in dominance (IAL-facet PA), assertiveness (NO), and competitiveness (BC), decreases in nurturance (LM) and introversion (FG).

b)[2,3] We predict *pre-post* changes in the following observer-rated personality states along the interpersonal circumplex: increases in dominance (PA), and competitiveness (BC), decreases in submissiveness (HI), and ingenuousness (JK); and in the following social impression dimensions: increases in self-assurance and self-display, decrease in cooperativeness.

3. a) In the experimental group only, we hypothesize associations of T reactivity with self-reported personality state changes: Positive for dominance (PA), assertiveness (NO), competitiveness (BC), negative for nurturance (LM) and introversion (FG).

   b)[2] Further, we hypothesize associations of T reactivity with observer-rated personality states and social impressions changes in the experimental group only: Positive for dominance (PA), cold-heartedness (DE), competitiveness (BC), self-assurance, and self-display, negative for nurturance (LM), submissiveness (HI), and cooperativeness.

4. a) In the experimental group we predict a relationship of T reactivity with self-reported personality state changes to be stronger when baseline C is lower (dual-hormone hypothesis, Mehta & Josephs, 2010). Specifically, we predicted larger increases for dominance (PA), assertiveness (NO), and competitiveness (BC), as well as larger decreases for nurturance (LM) and introversion (FG) with higher T reactivity and low baseline C.

   b)[2] Similarly, we predict baseline C to attenuate the relationship between T reactivity and the following observer-rated personality state and social impression changes: (positive) dominance (PA), competitiveness (BC), self-assurance, and self-display, (negative) submissiveness (HI), ingenuousness (JK) and cooperativeness.

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[2] There is no complete overlap in preregistered hypotheses between studies 2a and 2b, and 3a and 3b (all concerning observer-ratings): for Study 2a, there are only preregistered hypotheses concerning the two main axes' four facets (PA, HI, DE, LM), whereas 2b includes the facets PA, HI, BC, and JK. Study 3a, in contrast to 3b, does not include preregistered hypotheses regarding a TxC interaction. These differences are not theoretically based, but are simply due to slight differences in the initial study designs that were combined for this report.

[3] For 2a and 3a, observer ratings were collected for the experimental group only, for 2b and 3b, both groups were judged and hence differential changes between the experimental and control group could be hypothesized. These differences again are due to slight differences in the initial study designs.

Study 1

In Study 1, we investigated men's T reactivity (Hypothesis 1) and changes in self-reported personality states (Hypothesis 2) after a dyadic intrasexual competitive situation, as well as associations of personality state changes with T reactivity (Hypothesis 3) and the TxC interaction (Hypothesis 4).

Methods

Participants. We recruited 165 male heterosexual young adults with no hormonal disorders. There were 125 participants in the experimental and 40 in the control group[4]. Mean age was 24.3 years (*SD* = 3.2; experimental group: *M* = 24.1, *SD* = 3.3 years, control group: *M* = 24.9, *SD* = 2.9 years; overall range 18-34 years). The sample size in the experimental group (*n* = 125) had sufficient power (> .80) to detect effect sizes of Pearson's *r* > .24 (Cohen, 1992). In the experimental group, 59 indicated to be single, 66 in a relationship (10 open, 50 committed, four engaged, two married, none divorced or widowed; control group: 21 single, one open, 16 committed relationship, two married, none engaged, divorced or widowed). In the experimental and control group 90.4% and 82.5% were students, respectively (of which only two were enrolled as psychology students). On the 7-point Kinsey scale of sexual identity (1 = exclusively heterosexual to 7 = exclusively homosexual; Kinsey, Pomeroy & Martin, 1948), the mean was 1.19 (*SD* = 0.46). One participant indicated a bisexual orientation (Kinsey score = 4) and an unusually high number of sexual partners in the 12 months previous to the study, hence robustness analyses were conducted excluding him and any differences are reported. All procedures received ethics approval from the Georg-Elias-Müller-Institute of Psychology's Ethics Committee (no. 111).

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[4] Note: We had originally preregistered a sample size of *N* = 20 for the control group due to anticipated financial constraints. During data collection, we decided to increase the sample size to *N* = 40 for a more appropriate statistical power. This decision was not influenced by intermediate statistical analyses.

Procedure and Measures. To control for circadian variation in participants' hormonal reactivity, all testing was conducted between 2pm and 6pm (Idris, Wan, Zhang, & Punyadeera, 2017; Schultheiss & Stanton, 2009). The study was divided into two parts, a pre-session and a main session, with the latter happening a few days after the former.

Pre-session. During the pre-session, led by a male experimenter, participants provided informed consent, self-reports on interpersonal circumplex personality traits (using the Interpersonal Adjective List, Jacobs & Scholl, 2005), their sexual history and mating success (such as their relationship satisfaction (Sander & Böcker, 1993) and number of recent sexual partners; Penke & Asendorpf, 2008) were assessed, and body height and weight (to calculate BMI) were measured. A first saliva sample was taken approximately 20 minutes after arriving at the lab (to allow participants to calm down), in order to get a first measure of baseline T levels. Further measures not relevant to this study were also taken (see preregistrations). The pre-session was scheduled on a separate day to familiarize participants with the laboratory setting to avoid artificially increased hormonal levels during the main session (see Fales, Gildersleeve, & Haselton, 2014).

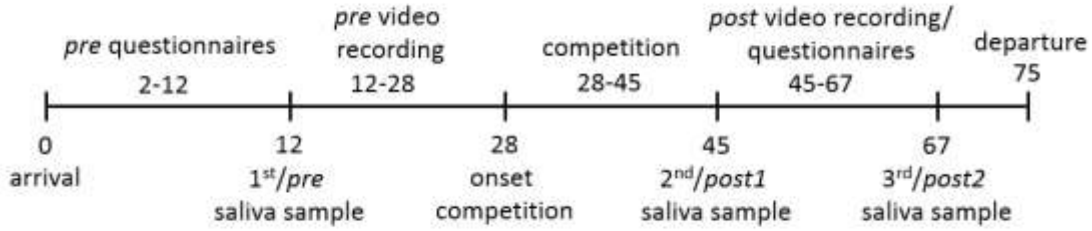

Figure 2. Timeline (in minutes) of the administration of the main session in the experimental group.

Main session. The main session's design included a *pre*- and a *post*-part (Figure 2), identical for the experimental and the control group. In the experimental group, two participants reported to the lab at a time, without meeting each other until the onset of the competition. First, participants filled out questionnaires on a computer. Personality states were assessed with a state version of the Interpersonal Adjective List (IAL; Jacobs & Scholl, 2005). Due to time constraints, the IAL was shortened to five out of eight items per facet (based on factor loadings and fit for the context of this study, 40 items total; see Table S1 for a list of items, and S2 for descriptive statistics). Participants also completed the following state questionnaires, which had been preregistered as control variables, next to age, BMI, recent sexual experience and relationship status: positive and negative affect (German version of the PANAS-X, 10 items each; Röcke & Grühn, 2003; Watson & Clark, 1994), stress (STAI, 6 items chosen from the full 20-item version; Spielberger, Gorsuch, Lushene, Vagg, & Jacobs, 1983) and state self-esteem (RSES, 4-item short version; Nezlek & Plesko, 2003). Approximately 12 to 15 minutes after arriving in the lab they provided a first saliva sample for baseline T and cortisol (C) measures. Afterwards, they were escorted into the video laboratory separately, one after another, to complete the first video recording. Then participants met each other and the female confederate, and engaged in the dyadic competition. Right after the competition, hence approximately 18-20 minutes after onset, a first *post*-saliva sample was taken, after which participants alternatingly completed further questionnaires including their personality states and the control variables (see above), and the second part of the video recordings. Finally, participants provided a second *post*-saliva sample (Figure 2). Two *post*-saliva samples were taken since it is not clear when exactly hormonal reactivity is highest and when changes are best detected in saliva. A delay of 15-20 minutes has been suggested for T responses (Casto & Edwards, 2016a; Schultheiss, Schiepe, & Rawolle, 2012). Moreover, Schultheiss and colleagues (2012) recommend to spread out multiple *post*-samples for measuring reactivity by at least 10 minutes, in order to leave time for the hormones passing into saliva after salivary glands have been filled up again. Our second *post*-sample was taken 20 minutes (on average, range ca. 18-30mins) after the first *post*-sample. Thus, our two *post*-samples can be interpreted as follows: The first *post*-sample can be seen as a measure of anticipatory reactivity (Marler, Oyegbile, Plavicki, & Trainor, 2005) and a T increase during the competition's first minutes. The second *post*-sample can be interpreted as representing T reactivity during the full competition phase and especially the two later disciplines (arm wrestling and turn-taking verbal fluency game, see below). For the control group, the procedure was very similar, except that participants completed the main session individually and instead of engaging in a competition watched a documentary video on Canada’s sustainable forests (SFM Canada, 2013), which was supposed to be neutral, free of social content, and not challenging, in order not to elicit a T response. The video had a duration of twelve minutes, thus roughly equivalent to the competition. Participants’ perception of the video documentary was assessed as a manipulation check, to see if the video was actually seen as neutral and non-challenging by the participants. Items were chosen to tap upon aspects which have been associated with T and C increases in previous studies (Goldey & van Anders, 2016; Hellhammer, Hubert, & Schürmeyer, 1985). The video was rated to be informative and below-average disquieting and stressful, and average in excitement, boredom and challenge (Table S2). Moreover, in the control group there was no female confederate present, the whole procedure was led by a male experimenter instead. After the second *post*-saliva sample, participants were debriefed about the study’s objective.

Hormonal assessments. Participants were asked to refrain from drinking alcohol, exercising, taking recreational or non-prescribed clinical drugs on the day of the study, from ingesting caffeine (coffee, tea, coke) or sleeping three hours before the study, and from eating, drinking (except for water), smoking or brushing teeth one hour before their scheduled appointment (Geniole, Busseri & McCormick, 2013; Lopez, Hay, Conklin, 2009). To check participants’ adherence to these instructions and to assess further potential influences on the saliva samples and hormonal levels, a screening questionnaire was administered at the beginning of the session (Schultheiss & Stanton, 2009). None of the participants indicated to be taking hormonal medication or supplements. For all saliva samples, participants provided at least 2ml of saliva via unstimulated passive drool through a straw (following the procedural guidelines provided in Schultheiss, Schiepe, & Rawolle, 2012; Fiers et al., 2014). The samples were immediately transported to an ultra-low temperature freezer (-80°C), where salivary T is stable for at least 36 months (Granger, Shirtcliff, Booth, Kivlighan, & Schwartz, 2004). At the end of data collection, saliva samples were shipped on dry ice to the Technical University of Dresden, where they were analysed using chemiluminescence-immuno-assays with high sensitivity (IBL International, Hamburg, Germany). The intra- and inter-assay coefficients (CVs) for C are below 8% and for T below

11%. Outliers were winsorized to 3 *SD*s (*n* = 8 in the experimental, *n* = 1 in the control group, in accordance with Mehta, Welker, Zilioli, & Carré, 2015; see also Pollet & van der Meij, 2017, for an extensive discussion of the influence of hormone outlier handling on significance testing). All T and C measures appeared to be positively skewed and to violate the assumption of normality (Shapiro-Wilk test statistics < .94, *p*s < .001). Consequently, all four variables were log10-transformed (see e.g., Mehta, Welker, Zilioli, & Carré, 2015). One participant in the experimental condition had missing data for baseline T and C, hence we could not calculate T reactivity and the TxC interaction (decreasing the sample size for these measures to *n* = 124). Thirty-one participants reported either recent gum bleedings or oral infections, which can lead to elevated steroid hormone concentrations (Schultheiss & Stanton, 2009). Testosterone and Cortisol levels were compared for these as a group with the remaining participants and no differences were detected (all unsigned *t*s < 1.58, *ps* > .11). To ease interpretation and comparison with other studies, hormonal values in these tables are reported in untransformed values (for T in pg/ml, C in nmol/l). The correlations amongst the two T *post*-measures were high (experimental/control group: *r* = .75/.89, *p*s < .001), suggesting moderate-to-high stability, comparable to previous results (Sellers, Mehl, & Josephs, 2007; Turan, Guo, Boggiano, & Bedgood, 2014). As expected, baseline T inversely predicted T reactivity for both *post*-saliva samples in the experimental group (*r* = -.44 and *r* = -.40, respectively, *p*s < .001; Roney, Simmons, & Lukaszewski, 2010).

Competition. Immediately before competition onset, participants filled out a short questionnaire assessing their motivation and expectation to win (Costa, Serrano, & Salvador, 2016). Participants competed in dyads in four disciplines, under supervision of the attractive female confederate, with the aim of eliciting a T response (e.g., Roney, Lukaszewski, & Simmons, 2007; Salvador & Costa, 2009). To increase participants' engagement in the competition, the winner of each discipline received an additional immediate monetary compensation of 2€, presented as a coin on the table during the discipline. For the four disciplines, a mixture of physical and cognitive tasks was chosen in order to increase the chances that the outcome of the competition remained undecided for longer (assuming a heterogeneity in talents): (1) a table pinball soccer game (played until one contestant had scored five goals), (2) a snatching game (where participants had to solve figural reasoning tasks, inferring which one out of five objects did not match two objects on cards in shape or color, and grasp the right object from the table quicker than the opponent, until one participant had won five rounds), (3) arm wrestling (best of three, alternating arms) and (4) a turn-taking verbal fluency task (where participants took turns naming words belonging to a certain category and starting with a specific letter, e.g., "occupations starting with *M*"; best of three). For all disciplines, see illustrations in the online supplementary material (Figure S2).

During all four disciplines, the female experimenter was told to interact naturally with the participants, while providing some verbal encouragement. The confederate had been carefully chosen for above-average physical attractiveness and communicative skills, heterosexual orientation, and age comparable to participants'. Her above-average physical attractiveness was confirmed in a pilot rating study (13 independent male raters judged a face and a full-body photo on four 7-point Likert scales from 1 = not at all attractive to 7 = extremely attractive; facial attractiveness: *M* = 5.15, *SE* = 0.27; bodily attractiveness: *M* = 5.46, *SE* = 0.27; overall short-term attractiveness: *M* = 5.69, *SE* = 0.31; overall long-term attractiveness: *M* = 4.77, *SE* = 0.47).

Video recordings. During the *pre* and *post* parts of both the experimental and the control group, self-presentation video recordings of participants were taken. Each participant was first told that the question he should answer within a one-minute time limit was, "What do you think, right now, is great about yourself?". Then he was presented with one of two sets of eight terms about "life domains" (Table S3) and instructed to choose three, which he would subsequently talk about. The life domains of the two sets were matched for equivalent meaning and presented in counterbalanced order, one in the *pre* and one in the *post* part (e.g., "humour" and "creativity"). The participants were given these terms as hints what to talk about and in order to ensure that they talked about of a variety of different, but roughly comparable things when presenting themselves. The three chosen domains were placed next to the camera, with the participant standing roughly four meters from the camera (to have a full-body view). Participants could start to speak whenever they felt like and gently reminded when they passed the time limit, but not stopped abruptly.

Statistical analyses. For personality state changes, difference scores were calculated for all IAL octants, with *pre*- subtracted from *post*-values (see Burt & Obradovic, 2012 for a detailed discussion of difference scores versus residuals). For T reactivity, percent changes from baseline levels (using the saliva sample obtained on the day of the main session) to *post*-levels were determined for both *post*-samples separately. The difference of *pre*- and *post*-levels were divided by baseline T (in accordance with Carré, Iselin, Welker, Hariri, & Dodge, 2014; Cook & Crewther, 2012; Roney, Mahler, & Maestripieri, 2003; van der Meij, Almela, Buunk, Fawcett, & Salvador, 2012). For all analyses described below, separate tests and models were employed for the two *post*-competition saliva samples. Concerning Hypothesis 1, to assess a potentially higher T reactivity in the experimental compared to the control group, linear regression models were employed, predicting T reactivity from the dummy-coded variable condition (0 = control, 1 = experimental condition), controlling for baseline T levels. Regarding Hypothesis 2, for personality state changes from before to after the competition (or watching the video in the control condition), comparing the two conditions, linear regression models were run, with personality state changes (for IAL octants separately) as the dependent variable, predicted by condition (0 = control, 1 = experimental condition), controlling for *pre*-personality states (Roney, Simmons, & Lukaszewski, 2010). Hypotheses 3 and 4 on the association between hormonal variables and personality state changes were performed on the experimental group only. To test the association between T reactivity and personality state changes, the latter were predicted by the former, controlling for *pre*-personality states and baseline T levels. For Hypothesis 4, the interaction between T reactivity and baseline C (TxC; using the baseline C measure obtained on the day of the main session) was added to test for moderating effects of baseline C. Since our studies were preregistered, we decided to use one-sided tests for our directional Hypotheses 1 to 4, marked with “one-tailed” (Cho & Abe, 2013; Lakens, 2016). For robustness checks, all models were again run including a range of preregistered control variables: age, BMI, relationship status coded as a binary variable (single versus partnered, the latter included those in an open or committed relationship, as well as engaged and married participants), recent sexual experience (binary, within previous 1 month) and *pre*-to-*post* changes in state positive and negative affect, stress, and self-esteem. Finally, as an exploratory analysis beyond our preregistration, we correlated participants' trait IAL scores with their baseline T values in order to replicate the finding of Turan, Guo, Boggiano and Bedgood (2014). Based on Turan and colleagues' results, we hypothesized a positive correlation of T with competitiveness (facet BC) and a negative correlation with the opposing facet ingenuous (JK). We also tested potential baseline TxC interaction effects on trait IAL facets, extending the replication of Turan et al. in line of the dual-hormone hypothesis (Mehta & Josephs, 2010). Analyses were performed using statistical softwares R (R Core Team, 2015) and SPSS Version 23, computerized versions of questionnaires were administered using formr.org (Arslan & Tata, 2017).

Data availability. The data and analysis scripts associated with this research are available at osf.io/8n7ev.

Results

Descriptive statistics for all main variables, and bivariate correlations between personality state changes and T reactivity can be found in Tables S4a and S4b. Internal consistencies (Cronbach's *α*) for the eight IAL facets (*pre* and *post* separately) ranged between .60-.85/.45-.89 for the experimental/control group (Table S4a).

Firstly, we attempted to replicate previously reported findings on associations between interpersonal circumplex traits and baseline T (Turan et al., 2014). In our sample (hypotheses were preregistered only for the PA facet, based on earlier findings on associations between T and dominance; e.g., Sellers, Mehl, & Josephs, 2007), no significant correlations between any IAL traits and baseline T were found (all *r*s < .11, *p*s > .18, *N* = 164; see Table S5), providing no support for Turan and colleagues' findings. In the following, results according to our preregistered Hypotheses 1 to 4 and analyses will be presented.

Hypothesis 1: T reactivity. For the first *post*-saliva sample (taken directly after the competition), but not the second (taken on average 20 mins after the first sample), T reactivity was higher in the experimental than control group (1st: $\beta = 0.44$, $p < .01$ (one-tailed), *partial* $\eta^2 = 0.04$; 2nd: $\beta = 0.26$, $p = .06$ (one-tailed), *partial* $\eta^2 = 0.01$). In the experimental group, T reactivity was higher for the second *post*-saliva sample than for the first T-sample. However, for the second T sample we also detected a significant rise in the control group (see Table S6). When including the preregistered control variables results remained virtually unchanged.

Hypothesis 2: *pre-post* changes in self-reported personality. Larger IAL personality state increases in the experimental relative to the control group were found for competitiveness (BC; $\beta = 0.41$, $p < .01$ (one-tailed), *partial* $\eta^2 = 0.04$; Table S7) and coldheartedness (DE; $\beta = 0.37$, $p = .03$, *partial* $\eta^2 = 0.03$), while ingenuousness (JK; $\beta = -0.41$, $p = .01$, *partial* $\eta^2 = 0.04$) decreased more in the experimental group (for the remaining facets, *p*s > .15). When including the eight control variables, all results remained virtually identical, except for the change in coldheartedness becoming non-significant ($p = .052$; Table S8). Looking at *pre-post* changes in the experimental group only, we detected increases in dominance (PA; $t = 2.23$, $p = .03$ (one-tailed), Cohen's d=0.20) and extraversion (NO; $t = 6.00$, $p < .001$ (one-tailed), Cohen's d=0.40), and decreases in submissiveness (HI; $t = -4.10$, $p < .001$, Cohen's $d = 0.28$), unassumingness (JK; $t = -4.33$, $p < .001$, Cohen's $d = 0.28$) and introversion (FG; $t = -5.19$, $p < .001$ (one-tailed), Cohen's $d = 0.38$; for the remaining facets, *p*s > .39).

Hypothesis 3: *pre-post* personality changes & T reactivity. In the experimental group, a positive association between T reactivity and personality state changes in competitiveness (BC) was detected for the first, but not the second *post*-saliva sample (1st: $\beta = 0.19$, $p = .02$ (one-tailed), *partial* $\eta^2 = 0.04$; 2nd: $\beta = 0.08$, $p = .18$ (one-tailed), *partial* $\eta^2 = 0.01$; see Table 1; Figure 3). When including the control variables results remained unchanged, except that an additional positive effect of T reactivity on changes in submissiveness emerged (HI; only for the second *post*-sample; $\beta = 0.20$, $p = .02$, *partial* $\eta^2 = 0.05$; Table S9).

Table 1

Results from linear models predicting personality state changes from T reactivity

IAL state changes	1st T reactivity (β)	*SE*	*P*	*Partial* η^2	2nd T reactivity (β)	*SE*	*p*	*Partial* η^2
Δ assured-dominant (PA)	.09	.09	.15[p]	0.01	.14	.09	.06[p]	0.02
Δ competitive (BC)	.19	.09	.02[p]	0.04	.08	.09	.18[p]	0.01
Δ coldhearted (DE)	.16	.09	.08	0.02	.01	.09	.90	0.00
Δ introverted (FG)	.01	.09	.47[p]	0.00	-.04	.09	.34	0.00
Δ submissive (HI)	-.01	.09	.91	0.00	.13	.09	.17	0.02
Δ ingenuous (JK)	-.15	.09	.10	0.02	-.14	.09	.13	0.02
Δ nurturing (LM)	-.12	.10	.11[p]	0.00	-.06	.10	.26[p]	0.00
Δ extraverted (NO)	.01	.09	.47[p]	0.00	.14	.09	.053[p]	0.02

Note. IAL = interpersonal adjective list; *SE* = standard error; partial η^2= partial eta-squared effect size;

[p] = one-tailed *p*-value due to preregistered hypothesis.

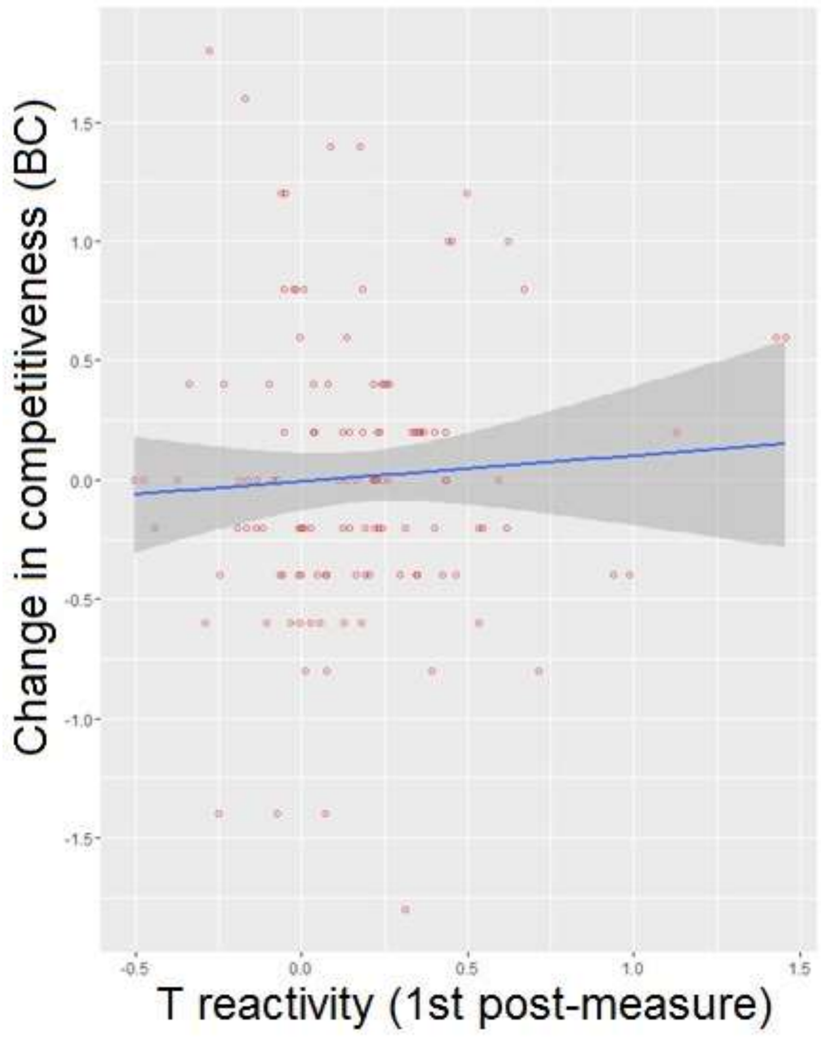

Figure 3. Pre-post changes in competitiveness (facet BC) predicted by the first T reactivity measure in the experimental group.

Hypothesis 4: *pre-post* personality changes & TxC interaction. A significant indirect effect of baseline C on personality state changes in competitiveness (BC; 1st: $β$ = -0.25, p = .01 (one-tailed), *partial* $η^2$ = 0.04; 2nd: $β$ = -0.20, p = .02 (one-tailed), *partial* $η^2$ = 0.03) and in dominance (PA; 1st sample only: $β$ = -0.20, p = .047 (one-tailed), *partial* $η^2$ = 0.02; 2nd: p = .19 (one-tailed); for the other facets, *p*s > .06; Table S10), moderating the effect of T reactivity, was found. In both cases, there was a positive relationship between T reactivity and change in competitiveness when baseline C was low, but a negative link when baseline C was high (Figure 4). When adding the control variables, results were unchanged for competitiveness, but the significant TxC interaction for dominance faded (p = .43^p; Table

S11). An additional significant moderating effect of baseline C on changes in coldheartedness (DE) for both *post*-saliva samples (1st: $\beta = -0.23$, $p = .02$, *partial* $\eta^2 = 0.04$; 2nd: $\beta = -0.20$, $p = .02$, *partial* $\eta^2 = 0.04$) emerged. As before with competitiveness and dominance, the link between change in coldheartedness and T reactivity was positive if baseline C was low, and negative if baseline T was high.

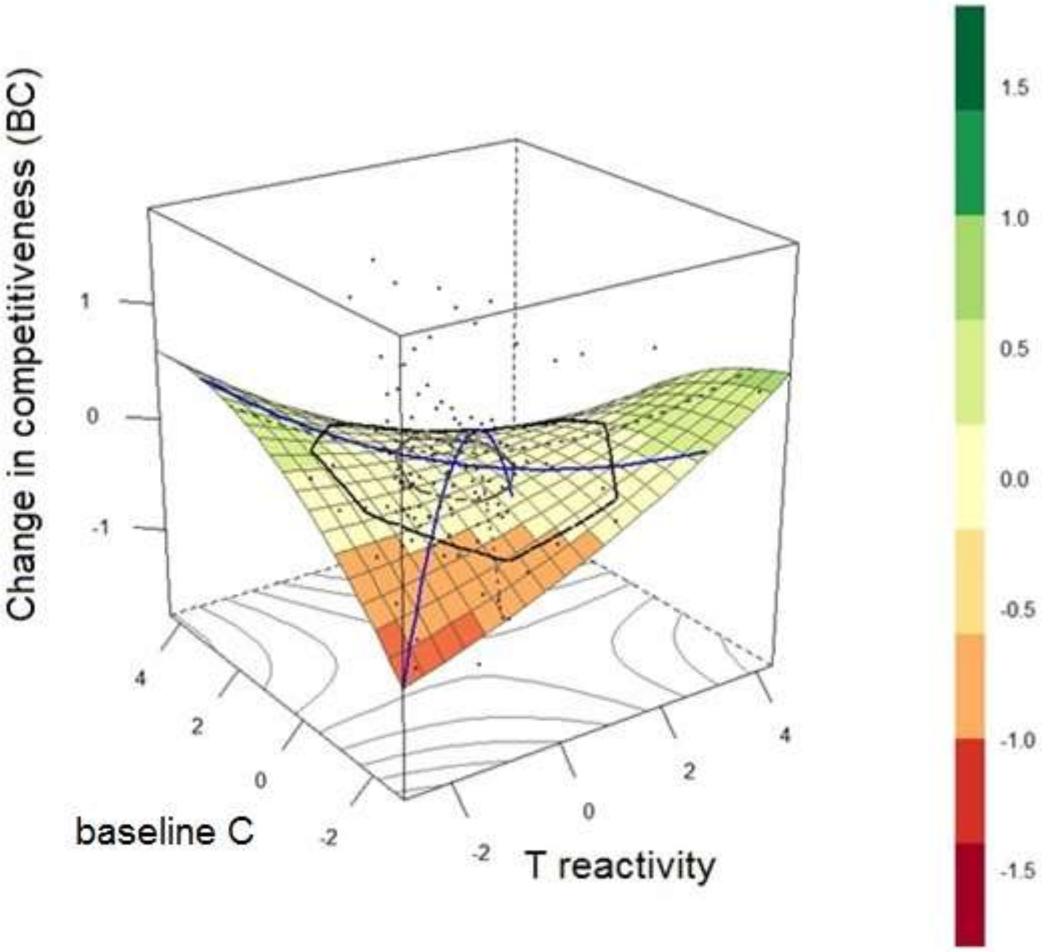

Figure 4. Interaction between T reactivity (first *post*-sample) and baseline C predicting the self-reported *pre-post* change in competitiveness (BC).

To conclude, we found a T reactivity for both *post*-saliva samples in the experimental group, which was even larger, relative to the control group, for the first, but not the second sample. Participants in the experimental group rated themselves to be more competitive (BC) and coldhearted (DE) and less ingenuous (JK) *post* compared to *pre*, relative to changes in the control group. The former change in the experimental group was positively predicted by participants' T reactivity, but only for the first *post*-saliva sample, not the second. For both *post*-saliva samples, this relationship was attenuated by high baseline C. We additionally found a TxC interaction on changes in dominance (PA; for the first *post*-saliva sample only). T reactivity was positively associated with higher changes in competitiveness and dominance, only if baseline C was low, in agreement with the dual-hormone hypothesis (Mehta & Josephs, 2010). Thus, all hypotheses received at least partial support.

Winner effect. We also attempted to replicate previous findings of a T increase in winners and a T decrease in losers, termed the "winner effect" (Geniole, Bird, Ruddick, & Carré, 2017). In this sample, we found no differential T reactivity depending on competition outcome (for both *post* T samples, unsigned βs < 0.21, *p*s > .22), only associations with personality state changes and effect of how close or decisive the competition outcome was on T reactivity (see Mehta, Snyder, Knight, & Lassetter, 2015; Table S36).

Moderators and mediators. Moreover, we tried to replicate a range of moderators and mediators of T reactivity which have been reported earlier. Previous studies showed an association of men's baseline T and/or T reactivity with female confederate's ratings of men's behaviour during a mating competition (Roney, Mahler, & Maestripieri, 2003; Slatcher, Mehta, & Josephs, 2011), their recent sexual activity within the previous one or six months (Roney, Mahler, & Maestripieri, 2003; van der Meij, Buunk, van de Sande, & Salvador, 2008), trait aggressive dominance (van der Meij et al., 2008), and relationship status (van der Meij et al., 2008). None of these replicated in our large sample of men (*N* = 118-165), except for single men having lower baseline T than those in a relationship (Table S37).

Actor-partner effects. Due to the dyadic nature of the participants' interaction, we ran actor-partner interdependence models (APIM; Kenny, Kashy, & Cook, 2006) using the AMOS 23 statistics programme. Here, the data of both competitors are analyzed simultaneously to control for a potential dependence amongst them, grouped into winners and losers of the competition. Effects on a focal participant’s personality state changes by the respective opponent’s T reactivity were investigated (Hypothesis 3), motivated by earlier findings on an association between baseline T levels and opponent’s dominant behaviour during a male dyadic mate competition (Slatcher, Mehta, & Josephs, 2011). Since in previous analyses we detected an effect of the first *post*-measure T reactivity on changes in self-reported competitiveness (BC), we will focus on these. The APIM models included both competitors’ T reactivities and changes in competitiveness. No partner effects were detected (winners’ T reactivity on losers’ BC change: β = -.03, *SE* = 0.23, *p* = .85; losers’ T reactivity on winners’ BC change: β = -.07, *SE* = 0.24, *p* = .60; see Figure S1). Hence, it can be concluded that for the association between personality state changes in competitiveness (BC) and T reactivity, no dependence amongst the two competitors was detected that could bias the results on an individual level, as reported above.

Further preregistered hypotheses. The results of further preregistered analyses (mainly on *pre-post* changes in further personality states, and their associations with baseline T, baseline C, and T reactivity) can be found in the online supplementary (Tables S39-S57).

Discussion. In Study 1 we demonstrate significant T increases in men after engaging in a dyadic intrasexual, female-led competition (replicating earlier findings of an acute T rise in the face of challenges such as mating opportunities and intrasexual contest; Archer, 2006; van der Meij, Buunk, van de Sande, & Salvador, 2008). In addition, we show that these hormonal fluctuations (T reactivity, relationships partly attenuated by high baseline C) are associated with personality state changes in dimensions relevant in such a competitive interaction (i.e., competitiveness and dominance), underlining previous suggestions of T modulating men’s competitive behaviour (Carre & Olmstead, 2015). However, these associations were significant mostly only for the first, but not the second T reactivity measure (except for the TxC interaction on competitiveness; Table 3), and only for one or two (Hypotheses 3 and 4, respectively) of the five preregistered circumplex facets (Table 3). Accordingly, they should be treated with care until further replication strengthens their robustness. In the following studies, we examine if these hormone-mediated personality state changes are detectable to naive observers, in order to test if hormonal responses trigger perceptible behavioural changes that can potentially function as social signals.

Studies 2 and 3

In preregistered studies 2 and 3, we tested if men's personality state changes from before to after an intrasexual competitive situation can be detected by observers based on thin slices of behaviour (Hypothesis 2), and if these state changes are associated with target men's hormonal changes (T reactivity, Hypothesis 3, and TxC interaction, Hypothesis 4). The thin slices are based on the video recordings from Study 1. In Study 2, target men's personality states were rated by females using the Interpersonal Adjective List (IAL; Jacobs & Scholl, 2005). Study 3 employed self-created social impression items (3 facets: self-assurance, cooperativeness, self-display) and both male and female raters. Both studies consisted of two parts: 2a and 3a only involved target men from Study 1's experimental group, and 2b and 3b additionally included the control group, in order to be able to test differential personality state changes between these two conditions, which we originally had not planned in 2a and 3a. Although simple observer-rated personality state changes in the experimental group (Hypothesis 2) could be of interest as well, relative changes compared to the control group are more revealing (as in 2b and 3b). This is since simple *pre-post* changes can at least partly be attributed to practice effects (target men speaking more fluently and feeling more confident in the *post* than in the *pre* video recordings and hence being judged differently). The comparison of *pre-post* changes with those in the control group theoretically enables us to partial out practice effects, as these should be present equally in both conditions. Moreover, in Study 3b, the wording of the social impression items has been improved. In Study 2a we used only three items per IAL facet (from the originally eight items), and each rater was asked to judge 24 items for each video. In 2b, we increased the number of items per facet to five (resembling the self-reports in Study 1), and these overall 40 items were divided into five item groups, so that each observer rated only eight items per video, clearly decreasing rater strain. Thus, the findings of both 2b and 3b should be seen as more reliable, since they represent improved and extended replications of 2a and 3a, respectively.

Study 2

Methods

Participants. Participants were 120 females (age: *M* = 23.8, *SD* = 2.6, range 19-31 years) in 2a and 400 females (age: *M* = 23.7, *SD* = 4.8, range 16-56 years) in 2b, all recruited via a local participant database. Raters' mean age was comparable to target men's mean age (*M* = 24.3 years).

Video-stimuli and procedure. Video-recorded self-presentations from Study 1 were used in this rating study (see above for details). All videos were cut to a maximum length of one minute. The videos of five participants in the experimental and two in the control group were removed from the stimuli sample due to audio problems, leaving a final stimulus set of *pre*- and *post*-videos each from *N* = 158 target men (*n* = 120 each for the experimental, *n* = 38 for the control group; length *M* = 53, range 10-62 sec.). Videos were distributed in a way so that the two videos of each target man never appeared together in the same set, to avoid direct contrast effects. Ratings were conducted in a computer laboratory on 24" screens using the software MediaLab v2014 (Empirisoft Corporation). Videos were presented in a randomized order.

Study 2a: stimuli and items. The video stimuli were divided into eight sets of 30 videos (experimental group only), of which half were *pre*- and the other half *post*-videos each. Each video was rated by fifteen independent female raters; participants rated 30 videos each. Participants were randomly assigned to one of the eight video groups. After every video 24 items were rated by each participant. As in Study 1, the German version of the Interpersonal Adjective List (IAL; Jacobs & Scholl, 2005) was employed. For reasons of brevity we used three out of the five items per facet that we had chosen for the self-ratings in Study 1 (overall 24 items; Table S1), which were rated on a 7-point Likert scale (1 = "disagree completely" to 7 = "agree completely").

Study 2b: stimuli and items. The video stimuli were divided into six sets of 40 videos and two sets of 38 videos each, of which half were *pre*- and the other half *post*-videos each. Each video was rated by ten independent female raters. Three-hundred and twenty of the raters viewed 40 videos and the remaining 80 rated 38 videos. Participants were randomly assigned to one of the eight video groups and to one of five item groups. Again, the German version of the IAL and all five items per facet (as in Study 1; Table S1) were employed; however, in order to reduce strain on our raters they rated the target men on only one of the five items per facet (a total of eight items per rater; each rater used the same eight items for the 38/40 videos). Overall target men were rated on 40 IAL items on a 5-point Likert scale (1 = "disagree completely" to 5 = "agree completely").

Statistical analyses. Analyses equalled those of Study 1, only substituting observer-ratings for self-reports. In 2a, only participants in the experimental group were included for Hypothesis 2.

Results

Bivariate Pearson correlations between observer-rated personality state changes and T reactivity, as well as descriptive statistics for all variables can be found in the online supplementary (Tables S12-S14). Internal consistencies (Cronbach's *α*) for the eight IAL facets (*pre* and *post* separately) ranged between .78-.98 (Study 2a) and .81-.95/.73-.95 for the experimental/control group in 2b (Tables S13-S14), and interrater agreements (Cronbach's *α*) for the eight facets were satisfactory to good (2a, *pre*: α = .79-.92, *post*: α = .85-.94, changes: α = .63-.77; 2b, *pre*: α = .85-.95, *post*: α = .89-.96, changes: α = .67-.87; Table S15).

Hypothesis 2: *pre-post* changes in observer-rated personality. In 2a, we detected a significant increase in observer-rated dominance (PA; t = 2.73, $p < .01$ (one-tailed), Cohen's d = 0.17) and extraversion (NO; t = 2.80, $p < .01$, Cohen's d = 0.22) and decreases in introversion (FG; t = -3.27, $p < .001$, Cohen's d = 0.21), submissiveness (HI; t = -2.97, $p < .01$, Cohen's d = 0.19) and ingenuousness (JK; t = -3.04, $p < .01$, Cohen's d = 0.19). In 2b we could partly replicate these results (increase in observer-rated dominance, PA: t = 2.77, $p < .01$ (one-tailed), Cohen's d = 0.15; decrease in introversion, FG: t = -2.59, p = .01, Cohen's d = 0.16; submissiveness, HI: t = -3.04, $p < .01$ (one-tailed), Cohen's d = 0.15; and ingenuousness, JK: t = -3.16, $p < .01$ (one-tailed), Cohen's d = 0.31), but not the increase in extraversion (NO, p = .72). Additionally, we found a significant increase in observer-rated competitiveness (BC; t =

2.88, $p < .01$ (one-tailed), Cohen's $d = 0.24$). A larger *pre-post* increase in the experimental compared to the control group was detected for dominance (PA; $\beta = 0.47$, $p < .01$ (one-tailed), $\eta^2_p = 0.04$; Table S16) and competitiveness (BC; $\beta = 0.35$, $p = .02$ (one-tailed), $\eta^2_p = 0.03$), and larger decreases for submissiveness (HI; $\beta = -0.52$, $p < .01$ (one-tailed), $\eta^2_p = 0.06$) and ingenuousness (JK; $\beta = -0.40$, $p = .01$ (one-tailed), $\eta^2_p = 0.03$). When adding the preregistered control variables age, relationship status and sexual orientation to the latter linear regression models results were unchanged (Table S17). For both 2a and 2b, we consistently found *pre-post* increases in dominance as well as decreases in submissiveness and ingenuousness in the experimental group.

Hypothesis 3: *pre-post* personality changes & T reactivity. In 2a, we found a significant positive link between change in dominance (PA) and T reactivity in the experimental group for the second hormonal *post*-sample ($\beta = 0.17$, $p = .04$ (one-tailed), $\eta^2_p = 0.03$), but not the first ($\beta = 0.12$, $p = .12$ (one-tailed), $\eta^2_p = 0.01$; for all others IAL facets, *p*s > .08; Table S18). The same result was obtained in 2b (second *post*-sample: $\beta = 0.17$, $p = .04$ (one-tailed), $\eta^2_p = 0.03$; first: $\beta = 0.13$, $p = .10$ (one-tailed); see Table 2). Results remained virtually identical when adding the preregistered control variables (Tables S19 and S20).

Table 2

Results from linear models predicting observer-rated personality state changes from T reactivity (Study 2b)

IAL state changes	1st T reactivity (*β*)	*SE*	*p*	*Partial* η^2	2nd T reactivity (*β*)	*SE*	*p*	*Partial* η^2
Δ assured-dominant (PA)	.13	.10	.10^p	0.01	.17	.10	.04^p	0.03
Δ competitive (BC)	.04	.10	.33^p	0.00	.11	.10	.13^p	0.01
Δ coldhearted (DE)	.07	.09	.44	0.01	.08	.09	.37	0.01
Δ introverted (FG)	.01	.10	.95	0.00	.02	.09	.87	0.00
Δ submissive (HI)	-.01	.10	.48^p	0.00	-.03	.10	.39^p	0.00
Δ ingenuous (JK)	.01	.10	.45^p	0.00	-.03	.10	.38^p	0.00
Δ nurturing (LM)	-.05	.09	.59	0.00	.00	.08	.97	0.00
Δ extraverted (NO)	.05	.10	.60	0.00	.08	.09	.42	0.01

Note. IAL = interpersonal adjective list; *SE* = standard error; partial η^2= partial eta-squared effect size; ^{p} = one-tailed *p*-value due to preregistered hypothesis.

Hypothesis 4: *pre-post* personality changes & TxC interaction. Testing for a potential moderation of the association between T reactivity and changes in observer-ratings by baseline C, no significant interactions were detected in either of the two parts (for the first/second T *post*-sample, 2a: unsigned *β*s < .15/.14, *p*s > .19; 2b: unsigned *β*s < .13/.08, *p*s > .17; Tables S21 and S22). Results were unchanged when including the control variables (Tables S23 and S24).

Discussion. In Studies 2a and 2b, we show that naïve female observers attribute personality state changes to men from before to after engaging in an intrasexual competition, which are partly linked to target men's T reactivity (but not to the TxC interaction). In both 2a and 2b, men were perceived to increase in dominance and decrease in submissiveness and ingenuousness (plus increases in extraversion in 2a and competitiveness in 2b, as well as decreases in introversion in 2a). In both 2a and 2b, increases in dominance were associated with T reactivity. However, we note that this association was significant only for the second, but not the first T reactivity measure, and only for one of four preregistered circumplex facets (in 2b; Table 3). Still, we provide some evidence that hormone-mediated personality state changes appear to be detectable to naive observers based on video-recorded thin slices of behaviour, suggesting that hormonal responses trigger behavioural changes, which may be functional in social signalling. Both Studies 2a and 2b employed only female observers, since we initially planned to focus on intersexual signalling effects (dominance- and competition-related behaviour) of T reactivity and associated personality state changes. In Study 3, we envisaged to examine changes in observer-perceptions in terms of more behaviourally phrased social impression items (self-display, self-assurance, cooperativeness). Since these social impression dimensions directly tap into facets implicated in men's intrasexual competition, mate attraction and affiliative behaviour (both intra- and intersexual signalling), we recruited male and female observers to investigate *pre-post* changes in social impressions and associations with T reactivity (and a TxC interaction).

Study 3

Methods

Participants. Eighty raters (40 females; age: *M* = 24.1, *SD* = 2.9, range 19-31 years) participated in 3a, and 160 raters in 3b (80 females; age: *M* = 24.5, *SD* = 4.9, range 16-53 years), all recruited via a local participant database. Again, raters' mean age was comparable to target men's average age (*M* = 24.3 years).

Stimuli and procedure. Stimuli and procedure were the same as in Study 2. There were eight video groups with 30 videos in 3a, and six sets with 40 videos and two sets with 38 in 3b (as in Study 2b). In 3a, each rater watched 60 videos and in 3b, 128 raters saw 40 videos and the remaining 32 saw 38 videos. For each video, nine items plus a question if the target was recognized (same as in Study 2) were rated for each target independently by ten male and ten female raters.

Items. Participants rated target men on three dimensions (self-display, cooperativeness, self-assurance) with three items each. In 3a, three positive items for each dimension were rated on a 7-point Likert scale (1 = “disagree completely” to 7 = “agree completely”), and in 3b two positive items and one inversed item were employed on a 5-point Likert scale (1 = “disagree completely” to 5 = “agree completely”; see Table S38 for a full list of items).

Statistical analyses. Analyses equalled those of studies 1 and 2. Difference scores were calculated for the three social impression dimensions. In 3a, only participants in the experimental group were included for Hypothesis 2.

Results

Descriptive statistics for all variables and bivariate Pearson correlations between observer-rated social impression changes and T reactivity can be found in the online supplementary (Tables S25-S27). Internal consistencies (Cronbach's *α*) for the three facets (*pre* and *post* separately) ranged between .94-.99 (3a) and .85-.97/.77-.98 for the experimental/control group in 3b (Tables S25 and S26). Interrater agreements (Cronbach's *α*) for the three facets were satisfactory to good (Study 3a, *pre*: *α* = .79-.92, *post*: *α* = .85-.94, changes: *α* = .61-.77; Study 3b, *pre*: *α* = .69-.89, *post*: *α* = .72-.88, changes: *α* = .42-.67; Table S28). Since for Studies 3a and 3b we employed male and female raters (as explained above), at first we assessed whether rater sex had a significant effect on the observer-ratings (Hypotheses 2-4). Rater sex was added as a covariate, and its interaction with condition (when analysing the differential *pre-post* change in 3b), with T reactivity and with the TxC interaction was investigated. In addition, for Hypothesis 2, only looking at the experimental group, Cohen's *d* effect sizes for *pre-post* changes for male and female raters were analysed for overlapping confidence intervals. We found no significant differences between male and female observer-ratings, neither regarding *pre-post* changes (all unsigned *t*s < 0.40; no overlap between males' and females' effect sizes in the experimental group), nor concerning T reactivity (all unsigned *t*s < 0.96) or the TxC interaction (all unsigned *t*s < 1.22). Since we detected no effect of the sex of the raters, we will present results with observer ratings aggregated across male and female raters.

Hypothesis 2: *pre-post* changes in observer-rated social impressions. For 3a, in the experimental group we found an increase in observer-rated self-display (*t* = 3.53, *p* < .001 (one-tailed), Cohen's *d* = 0.28) and self-assurance (*t* = 3. 92, *p* < .001, Cohen's *d* = 0.22), but not cooperativeness (*t* = -0.22, *p* = 41 (one-tailed), Cohen's *d* = .02), which we could entirely replicate in 3b (self-display: *t* =

3.19, $p < .01$ (one-tailed), Cohen's $d = 0.24$; self-assurance: $t = 3.73$, $p < .001$ (one-tailed), Cohen's $d = 0.2$; cooperativeness: $t = -1.33$, $p = .09$ (one-tailed), Cohen's $d = 0.13$). Looking at the differential *pre-post* changes in the experimental and control groups (3b), we again found a higher increase in both self-display ($\beta = 0.29$, $p = .046$ (one-tailed), $\eta^2_p = 0.02$) and self-assurance ($\beta = 0.35$, $p = .02$ (one-tailed), $\eta^2_p = 0.02$), but not cooperativeness ($p = .45$ (one-tailed)). These results were robust when adding the preregistered control variables age, relationship status and sexual orientation (Table S29).

Hypothesis 3: *pre-post* changes in social impressions & T reactivity. In the experimental group of both 3a and 3b, we found a positive association between changes in observer-rated self-assurance and T reactivity for the first hormonal *post*-sample (3a: $\beta = 0.19$, $p = .03$ (one-tailed) $\eta^2_p = 0.03$; 3b: $\beta = 0.19$, $p = .03$ (one-tailed), $\eta^2_p = 0.03$), but not the second ($\beta = 0.11$ and $\beta = 0.15$, respectively, *p*s > .055 (one-tailed); for self-display and cooperativeness, *p*s > .08 (one-tailed); Tables S30 and S31). Results were virtually unchanged when adding the preregistered control variables age and relationship status (3a) as well as and sexual orientation (3b; Tables S32 and S33)

Hypothesis 4: *pre-post* changes in social impressions & TxC interaction. No significant interaction between T reactivity and baseline C, hence no moderation of the association between T reactivity and changes in observer-ratings by baseline C, was detected (for the first/second T *post*-sample, 3a: *p*s > .051; 3b: *p*s > .09; Tables S34 and S35).

Discussion. In both studies 3a and 3b, target men were perceived to increase in self-display and self-assurance by naïve observers after, relative to before, engaging in an intrasexual competition. The observer-rated increase in self-assurance was higher for target men showing a larger T reactivity (no association with TxC interaction). Hence, we demonstrate T-modulated changes in social signalling, not only in terms of interpersonal personality states (Studies 2a and 2b), but also in terms of more concretely phrased social impression items, in domains relevant in men's inter- and intrasexual competition.

Table 3

Overview of results for preregistered hypotheses for Studies 1, 2b and 3b

	Self-reports	Observer-ratings	
Hypotheses	IAL	IAL	Social impressions
1) T reactivity[a]	1st, not 2nd T *post*-sample		
2) personality state changes[a]	competitiveness (BC), coldheartedness (DE)[c], ingenuousness (JK)[c]	dominance (PA), competitiveness (BC), submissiveness (HI), ingenuousness (JK)	self-display, self-assurance
Not supported for:	dominance (PA), extraversion (NO), nurturance (LM), introversion (FG)	-	cooperativeness
3) personality state changes & T reactivity[b]	competitiveness (BC; 1st, not 2nd T *post*-sample)	dominance (PA; 2nd, not 1st T *post*-sample)	self-assurance (1st, not 2nd T *post*-sample)
Not supported for:	dominance (PA), extraversion (NO), nurturance (LM), introversion (FG)	competitiveness (BC), submissiveness (HI), ingenuousness (JK)	cooperativeness, self-display
4) personality state changes & TxC[b]	competitiveness (BC; 1st & 2nd T *post*-sample), dominance (PA; 1st T *post*-sample only)	-	-
Not supported for:	dominance (PA), extraversion (NO), nurturance (LM), introversion (FG)	dominance (PA), competitiveness (BC), submissiveness (HI), ingenuousness (JK)	cooperativeness, self-display, self-assurance

Note. T = testosterone, TxC = T reactivity x baseline C interaction, IAL = interpersonal adjective list, [a]relative changes, experimental versus control group, [b]experimental group only, [c]hypothesis not preregistered.

General Discussion

Across three preregistered studies, we investigated the association between self-reported and observer-rated personality state changes and hormonal reactivity in men in an intrasexually competitive context. Several interesting findings regarding the interplay of personality and hormones emerged. Firstly, an increase in testosterone (T) was detected from before to after competing against another male participant while being supervised by an attractive female confederate. The increase was partly (for the 1st, but not the 2nd *post* T sample) significantly higher than in a control group, in which men only watched a neutral documentary and were supervised by a male experimenter. Secondly, in

Study 1, *pre-post* increases in self-reported personality state facets competitiveness (BC)[5] and coldheartedness (DE) of the Interpersonal Circumplex (Wiggins, 1982; Figure 1), and decreases in ingenuousness (FG) were found (experimental relative to control group). Concerning observer-ratings on the interpersonal circumplex (Study 2b), larger increases in the experimental compared to the control group for dominance (PA) and competitiveness (BC), and larger decreases for submissiveness (HI) ingenuousness (JK) were found. Regarding the three social impressions (Study 3b), *pre-post* increases in observer-perceived self-display and self-assurance, but not cooperativeness, were larger in the experimental than in the control group. Note that concerning the association between T reactivity and self-reported personality state changes, a positive link emerged of T reactivity with changes in competitiveness for the first, but not the second *post* T sample. For observer-rated states, changes in dominance were positively related with the second, but not first T reactivity measure. Regarding social impressions, increases in self-assurance were linked with a higher T reactivity for the first, but not second *post* T sample. We will discuss this pattern below. Dyadic effects between both participants' T reactivity and self-reported personality state changes were investigated employing actor-partner interdependence models (APIM; Kenny, Kashy, & Cook, 2006). No effects on a focal participant's personality state changes by the respective opponent's T reactivity were revealed, thus questioning potential partner effects (as reported for dominance behaviours by Slatcher, Mehta & Josephs, 2011). Finally, an interaction between T reactivity and baseline C on changes in self-reported competitiveness (for both *post* T samples) and dominance (for the first sample only) was found in the experimental group. That is, associations between T reactivity and changes in competitiveness and dominance were attenuated by high baseline C. No TxC interaction emerged for the observer-perceptions, for neither circumplex personality states nor social impressions.

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[5] The facet is originally called "arrogant-calculating" (Horowitz, Wilson, Turan, Zolotsev, Constantino, & Henderson, 2006). Since we selected five out of the overall eight items of the facet BC, with the final set of items including "competitive", "provocative" and "belligerent", and given our study's intrasexually competitive context, we decided to re-label the facet to "competitiveness". This is, of course, only descriptive, and our interpretation concerning this facet would equally apply when using the label "arrogant-calculating".

Thus, employing a relatively large sample of men (*N* = 165), we show preregistered associations between post-competition T reactivity and personality state changes, which are not only self-reported, but also perceived by naive observers. The T increase, which was partly larger in the experimental group following a competitive interaction than in the control group, is in line with predictions derived from the challenge hypothesis (Archer, 2006; Wingfield, Hegner, Dufty Jr, & Ball, 1990), replicating previous studies in the realms of intrasexual competition and female exposure (e.g., Roney, Lukaszewski & Simmons, 2007; van der Meij, Buunk, Almela, & Salvador, 2010).

Moreover, personality state changes were detected in our intrasexually competitive context, which mostly support our preregistered hypotheses (as outlined above; see Table 3). Regarding the interpersonal circumplex, changes in self-reports and observer-ratings overlap for competitiveness and ingenuousness. Interestingly, observer-perceptions also changed on both endpoints of the Dominance main axis (dominance and submissiveness), whereas self-reports increased *pre-post* on the negative endpoint of the Love axis (coldheartedness). Thus, we see somewhat diverging changes for participants' own reports and observer-ratings. These might be meaningful, in that while (changes in) dominant personality states are more perceptible externally (related to boldness and self-assurance - for the latter social impression facet we also saw changes in observer-ratings), changes in coldheartedness may be more an internal process, with no clear associated differences in mimics or gestures, which would be observable by raters. There is some evidence that certain personality facets, such as extraversion, are being judged with higher accuracy than more internal facets, such as openness to experience (Ambady, Bernieri, & Richeson, 2000). However, importantly, in our case we are not primarily interested in accuracy (in terms of overlap between target and informant), only in changes from baseline to a hormonally aroused state. Thus, so far we can only say that changes in coldheartedness seem to be more salient to oneself, and changes in dominance and submissiveness more to observers. Changes in these personality facets may well be adaptive in competitive situations (Dall, Houston, & McNamara, 2004), and map onto a behavioural spectrum of competition versus nurturance, which has been suggested for effects of T (van Anders, Goldey, & Kuo, 2011).

Implications for the role of T in mate acquisition and intrasexual competition

Hence, in our study we showed that T indeed rose in the face of an intrasexual competition combined with a female exposure. T reactivity also appeared to be linked with personality state changes in domains relevant to this intrasexual competitive context. Since these personality dimensions relate to aspects of social status (Eisenegger, Haushofer, & Fehr, 2011; Mattan, Kubota, & Cloutier, 2017), our findings converge with predictions from the biosocial model of status (Mazur 1985, 2015; Mazur, Welker, & Peng, 2015), according to which fluctuations in status should be linked to T levels. Moreover, these associations fit well into previous claims of acute T fluctuations playing a crucial role in men's mating efforts and intrasexually competitive behaviour, by hinting at a potential trade-off between competitive versus nurturing behaviour, which seems to be reflected in changes in interpersonal personality states. In addition, these T-modulated personality state changes were not only reported by oneself, but also recognized by naive observers. The latter fact may mean that these personality state changes associated with T fluctuations function as an intrasexual competitive signal detectable by observers, further supporting status competition and/or mate acquisition. On an evolutionary functional level (Tinbergen, 1963), this shows that both personality state changes and hormonal reactivity might play a crucial role in supporting important aspects of men's striving for a high reproductive success. This trade-off surrounding T variability in men can be embedded in a larger set of trade-offs in the realm of human reproduction. According to life history theory, an individual faces a range of trade-offs of allocating effort (especially time, energy and resources) to tasks and traits in the pursuit of optimal fitness (Del Giudice, Gangestad & Kaplan, 2015). One such trade-off, which has been suggested to be regulated by acute T levels, is between mating and parental effort (Muehlenbein & Bribiescas, 2005) and should translate into competitive versus nurturing behaviours, with high T being related to the former (e.g., status acquisition) and low T to the latter (e.g., pair bonding) (van Anders, Goldey, & Kuo, 2011). We were not able to replicate earlier findings of inter-individual associations between dominant, competitive or nurturing personality traits and baseline T (Turan, Guo, Boggiano; & Bedgood, 2014; Sellers, Mehl, & Josephs, 2007). This is in line with Simmons and Roney's (2011) null-finding of a link between baseline T and three measures of intrasexual competitiveness (self-reported dominance and prestige as well as physical strength) in men (*N* = 149). To further clarify potential relationships on an inter-individual difference level, alternative sampling methods, such as from hair (Dettenborn et al., 2016) or fingernails (Matas & Koren, 2016) could be employed. These can potentially provide more stable and long-term aggregated hormonal measures, and hence potentially more valid accounts of baseline T. So far, our results corroborate the idea that there may be no strong and consistent links between T and personality on a stable trait level, and that personality and behavioural effects of T reactivity are stronger, compared to baseline T (Carré & Olmstead, 2015). In support, we found that variability in competitive personality states was positively related to men's T response, hence on an intra-individual level.

Similarly, the interaction of T and C (a buffering of the association between T reactivity and increases in competitiveness and dominance by high baseline C) can be interpreted in light of the life history theory. In particular, in times of high stress, C levels tend to be elevated, and reproductive effort decreases (Del Giudice, Ellis, & Shirtcliff, 2011). Consequently, the status-seeking effects of increased T levels are attenuated in times of high stress, to limit an individual's extensive spending of resources and risky behaviour, in order to ensure survival. Thus, T reactivity in response to intrasexual challenges and mating opportunities may be one of many mechanisms in the calibration of immediate personality and behaviour, depending on contextual cues and the availability of resources, to achieve a high inclusive fitness, particularly in men (for an extensive review, see Gray, McHale, & Carré, 2017).

Observer-perceptions of T-mediated behavioural changes

We additionally demonstrated personality state changes perceptible by naïve observers based on short video recordings (thin slices of behaviour; Borkenau, Mauer, Riemann, Spinath, & Angleitner, 2004). The observers showed a moderate to high interrater agreement for both *pre* and *post* videos, and consensus was only slightly lower for *pre-post* changes. So far, it was unclear whether and how hormone-mediated behavioural changes are perceived by male and female observers outside the immediate competitive context at all (Mattan, Kubota, & Cloutier, 2017). Some previous studies have coded and rated behavioural facets and analysed these in association with baseline T and/or T reactivity. In previous female exposure studies, men's T reactivity was found to be related to female-perceived self-presentation behaviour (van der Meij, Almela, Buunk, Fawcett, & Salvador, 2012) and female confederate's rating of how much the males tried to impress her (Roney, Mahler, & Maestripieri, 2003). Our results regarding the link between T reactivity and *pre-post* changes in observer-perceived dominance and self-assurance strongly support these, only that we were not looking at absolute behaviours, but behavioural changes. Moreover, these findings support previous interpretations of T increases being linked to status-seeking and -maintaining behaviours in a competitive context in men (Anderson & Kilduff, 2009; Eisenegger, Haushofer, & Fehr, 2011; Mehta & Josephs, 2010). We thus provide clear evidence that on the dimensions self-assurance and dominance in particular, T-modulated behavioural changes are noticed by observers outside the original competitive context. Cooperativeness, however, appears to be rather orthogonal to the other two dimensions, at least in the interpersonal circumplex model (Wiggins, 1982). Consequently, it may be that T is only related to dominance, but unrelated to cooperativeness. Alternatively, since T reactivity was associated with self-reported changes in the facet between the Dominance axis and negative endpoint of the Love axis (i.e., competitiveness), it may well be that indeed state changes on a facet closely related to cooperativeness happened, but were not perceived accurately by observers. Similar associations between warmth and nurturance, and low T have been proposed earlier (van Anders, Goldey, & Kuo, 2011). Finally, in some contexts, cooperativeness has been positively linked to T levels (e.g., in-group cooperation during inter-group competition; Reimers & Diekhoff, 2015). Since cooperativeness has been linked with both high and low T values depending on contextual variables, the null findings of our Studies 3a,b are not surprising. Target men were not instructed to behave in a conflicting way. Consequently, they did not seem to have emitted specific signals, which were perceived and interpreted accordingly by observers. Thus, it would be interesting to study how target men's behaviour would change in different settings, for example a competitive group task, and how this would be judged by observers.

Effects for self-reports in association with T reactivity were found not for any of the two interpersonal circumplex model's main axes, Dominance and Love, but for the facet in between Dominance and the negative pole of Love, competitiveness. For observer-perceptions, in contrast, the main axis Dominance was positively associated with T reactivity, alongside social impressions of self-assurance. These seem complementary, since all fit well in an intrasexually competitive context. The differential findings for self-reports and observer-perceptions could be interpreted in such a way that T fluctuations are related more to self-reported personality aspects of status-seeking (competitiveness), and observer-ratings more to confidence and hence current status (dominance and self-assurance, but not self-display, which would more fit into attempts of status-seeking; Hays & Bendersky, 2015). Of course, replications are called for, to see whether this slight differentiation regarding self-reports and observer-perceptions holds. Overall it can be concluded that most of the effects were located on the Dominance main axis and the competitiveness facet (as well as related social impressions), but not so much on the Love main axis, and not at all on the extraversion-introversion axis. This further corroborates the relevance of a T-modulated trade-off between mating and parental effort (e.g., Muehlenbein & Bribiescas, 2005; Muller, 2017; Zilioli & Bird, 2017), and associations along a competition-nurturance dimension (van Anders, Goldey, Kuo, 2011).

Testosterone x Cortisol interaction

Associations between men's T reactivity and increase in self-reported competitiveness and dominance were attenuated by high baseline C. This finding of a TxC interaction further corroborates previous reports that C may inhibit effects of T on status-related behaviours (e.g., Mehta, Welker, Zilioli, & Carré, 2015; Mehta & Prasad, 2015; Sherman, Lerner, Josephs, Renshon, & Gross, 2016). Especially the finding regarding changes in dominance is exactly in line with the original study proposing the dual-hormone hypothesis (Mehta & Josephs, 2010), in that the positive relationship between dominance and T was only significant with simultaneously low C levels, which we showed for personality state changes and hormonal reactivity. Since we found a TxC interaction on changes in self-reports, but not observer-perceptions, it appears the buffering of T effects by baseline C is not related to perceptible state changes, in contrast to effects associated with T reactivity (changes in dominance and self-assurance). The moderation of the link of increases in self-reported competitiveness and dominance with T reactivity by baseline C can be interpreted in such a way that a T increase, as experienced in a competitive situation, is only converted into stronger status-seeking personality states when there is no shortage of available resources (i.e., low stress; Sherman, Lerner, Josephs, Renshon, & Gross, 2016). Hence, baseline C functions as a regulator between competition-induced T fluctuations and personality state changes. However, it is not a complete gatekeeper, since we found main effects of T reactivity on changes in competitiveness as well (see Hamilton, Carré, Mehta, Olmstead, & Whitaker, 2015). Even when including baseline C without the TxC interaction in the model predicting changes in competitiveness, the effects of T reactivity (for the first *post*-sample) prevailed (no main effect of T reactivity was found for dominance). This shows that even though the effects of T reactivity were stronger when baseline C was low, activation of the hypothalamus pituitary gonadal (HPG) axis was still related to these personality state changes when controlling for baseline hypothalamus pituitary adrenal (HPA) axis activation (van Anders, Steiger, & Goldey, 2015). Thus, we provide further evidence for the dual-hormone hypothesis, at least for self-reports, and in terms of changes in competitive and dominant personality states.

Trait activation in a competitive context

The increases in competitiveness-related personality states we found can also be interpreted in terms of trait activation, since these personality dimensions fit well with the competitive context we created in the lab. According to trait activation theory, individuals express their personality traits when confronted with situational cues relevant to these traits (Tett & Burnett, 2003). In our study, aspects of the situation like being challenged by the competition, having the opportunity to win over another man and earn a monetary reward, and the presence of the attractive female may have functioned as primarily task-related and social cues (Tett & Burnett, 2003). Here, personality state changes can be seen as the primary manifestations of trait activation, with T reactivity as the underlying physiological mechanism. In the current study, we primarily wanted to make sure that T reactivity was triggered by our experimental manipulation of the lab situation, so we purposely combined several situational features that had been shown in the literature to trigger a T response, including a competitive intrasexual challenge with no immediately clear winner and exposure to a potential mate. To further disentangle which particular aspects may have triggered the personality state changes and T reactivity, future studies could employ more fine-grained control groups, such as staging a competition, but not involving a female confederate, or a non-competitive interaction between two men, simply substituting the female confederate by a male experimenter, or varying the female confederate's attractiveness. This could also shed some light upon which aspects of the competitive situation activate which personality dimensions and have the most influence on T reactivity exactly (cf. Edelstein, Yim, & Quas, 2010; Roney, 2016).

Most of our significant associations between personality state changes and T reactivity were detected for the first, but not the second *post*-sample (Table 3). We chose to employ two *post* measures, since from previous studies it was not entirely clear when T reactivity was highest (Schultheiss, Schiepe, & Rawolle, 2012), and previous studies were heterogeneous concerning the timing of reactivity measures (from immediately to 1 hour after a competition's end; Casto, Elliott, & Edwards, 2014; Trumble et al., 2012). Based on claims of a delay of 15-20 minutes for hormonal reactivity to be detectable in saliva (Schultheiss, Schiepe, & Rawolle), our findings could be interpreted as follows: changes in self-reported competitiveness and in observer-rated self-assurance are linked with anticipatory reactivity (Marler, Oyegbile, Plavicki, & Trainor, 2005) and a T increase during the competition’s first minutes. Increases in observer-perceived dominance, in turn, relate to T reactivity during the full competition phase and especially the later disciplines. Of course, these interpretations should be treated with care, since there is large intra- and inter-individual variations in hormonal levels (especially diurnal declines; Schultheiss & Stanton, 2009), so further studies are required to see if these represent meaningful differences (Casto & Edwards, 2016a,b). Overall, from our findings we could also conclude that the first *post*-sample was timed better for detecting relationships with personality state changes, and future studies may follow the protocol of assessing T reactivity slightly earlier.

An influential variable in previous studies was the competition's outcome, derived from the biosocial model of status. According to the "winner effect", winners increase and losers decrease in their T levels after competitions (or at least the T increase is larger in winners, compared to losers; Casto & Edwards, 2016a). However, in our study we detected no differential associations by outcome, neither in terms of larger T increases in winners, nor consistent interactions of outcome with T reactivity on self-reported personality state changes (though some effects were found for observer-ratings; see Table S36). These are only partly in line with predictions from the biosocial model of status and contradict a recent meta-analysis on the winner effect by Geniole and colleagues (2017). Van der Meij and colleagues (2010) suggested rather than actual outcome, perceived outcome, which would depend on cognitive and contextual factors (e.g., self-efficacy; the competition's setting, or the "home advantage"; Fuxjager, Mast, Becker, & Marler, 2009; but see Fothergill, Wolfson, & Neave, 2017), would more likely impact T reactivity. In our study, T reactivity was associated with how close or decisive the outcome was, in that T responses were larger after close than decisive outcomes. This could be explained by contestants having perceived the competition as more challenging and been more engaged when the level of skills within a dyad was similar across disciplines, which might have triggered a larger T reactivity. In further studies, contestants' perceived degree of being challenged and engaged in a competition could be assessed, which, given our theorizing received support, would nicely corroborate the challenge hypothesis. Thus, while a competition outcome's decisiveness may well influence subsequent T fluctuations, the outcome was more associated with personality state changes, but not T reactivity, in our study. As a consequence, one proposed key aspect of the social environment, objective competition outcome, may not be as influential as suggested by the biosocial model of status and previous studies. Instead, T reactivity more generally translates into more competitive self-perceptions and making a more dominant and self-assured impressions on others in winners and losers alike (Carré & Olmstead, 2015).

Strengths and limitations

Compared to the social endocrinology literature and considering the rather complex design, we recruited a large sample, providing relatively high statistical power to detect significant effects. We also recruited a very large number of male and female raters for the video ratings and replicated results for the observer ratings across multiple rater groups and operationalizations (adjective and social impression ratings). Moreover, we used a multi-method approach including physiological measures, self-reported and observer-judged personality states based on questionnaires and video recordings (Vazire, 2006), allowing us to comprehensively study the association between hormones and personality from different angles. We considered not only isolated effects of a single hormone (T), but also the interaction with a second hormone (C), since often it is co-released endocrine signals that affect behaviour and personality (Roney, 2016). Furthermore, we implemented a control group to check for changes in perceived personality states and social impressions due to practice effects from *pre* to *post* video recordings. However, further research could examine more fine-grained control groups, to analyse differential effects of the competition and female exposure (as discussed above). Our dyadic competition was composed in such a way that it presumably was at least somewhat relevant to all participants, since we employed a mixture of cognitive and more physical disciplines. Men with different skill sets should have perceived similar chances to win the competition. We selected disciplines in which participants could be expected to not have too much experience (e.g., table pinball game rather than simple foosball, since the former is less common). We designed our competition to be as competitive as possible, with opponents being seated directly opposite each other, and presumably being motivated by the monetary incentives and presence of the attractive female (van der Meij, Buunk, Almela, & Salvador, 2010). The T reactivity and personality state changes we found relative to the control group indicate that our manipulation was successful. Finally, results concerning the effects of our competition can be seen as at least as or even more generalizable than previous findings, since we employed a more realistic and natural kind of competition (including a classic "male" competitive discipline, arm wrestling), compared to computerized tasks such as the Point Subtraction Aggression Paradigm (Carré, Putnam, & McCormick, 2009). In addition, our competition outcome emerged naturally (being more credible for the participants than rigged competitions; e.g., Geniole, Busseri, & McCormick, 2013). Still, our study took place in a laboratory setting, which often shows a limited but satisfactory generalizability (Sherman, Lerner, Josephs, Renshon, & Gross, 2016), so that replications in more natural contexts may be required.

Regarding the limitations, it has been questioned to what extent salivary T is a good estimate of free unbound T as measured in serum, thus potentially limiting the validity of our findings. However, Fiers and colleagues (2014) recently pointed out measurement bias may be less influential in men than in women, due to lower T levels in the latter. Moreover, a superior validity of salivary measurement using passive drooling (as in our study) was shown compared to salivettes. We conducted the saliva collection with great care following a strict procedure (e.g., Granger, Shirtcliff, Booth, Kivlighan, & Schwartz, 2004), subsequently storing the samples at -80°C (where hormone levels are stable for years; Granger et al.), and assessed a wide range of confounding variables (Schultheiss & Stanton, 2009). Besides the significant T reactivity for both *post*-samples in the experimental group (relative to baseline T), we also detected a significant T increase in the control condition for the second (but not first) sample. It is rather unlikely this can be explained by the participants' watching the documentary video, since the documentary was rated to be informative, but average on items such as challenging, exciting, boring, and significantly below the midpoint of the scale for disquieting and stressful. Rather, the T increase may be ascribed to participants being stressed and challenged by the video-recorded self-presentation, especially since the question was framed in a challenging way ("What is great about yourself?"). This is corroborated by the fact that these participants also showed a C increase. Since greater T and personality state reactivity was shown in the experimental compared to the control group and further analyses involving T reactivity focussed on the experimental group, the control group's T reactivity does not constitute a serious issue. Still, we show how relatively little manipulation is necessary to induce a hormonal response, especially in the control group, and only exactly why T increased here remains inconclusive.

Concerning some self-reported personality state facets we have to acknowledge only moderate internal consistency (especially competitiveness and ingenuousness; Table S4a). This can likely be ascribed to item selection, since instead of the originally eight items per facet (Jacobs & Scholl, 2005) we selected five, also for reasons of brevity. This limitation calls for replication using the full facets. Finally, it is important to acknowledge that analyses of correlated changes, such as in this study on personality state changes and hormonal reactivity, are statistically difficult. Despite comparably large sample size, power to detect such effects was only moderate. Consequently, even though our results are theoretically sound, they need to be taken with care until further replication.

Future research

There is an abundance of possible pathways to further elucidate hormonal and personality state changes as well as their associations in intrasexually competitive contexts. First of all, this study was restricted deliberately in terms of age (focussing on participants presumably active on the mating market and hence especially responsive to an attractive female confederate) and sex (only males). To assess the generalizability of our findings beyond these, similar studies could be conducted in different samples. Even though T supposedly plays a more minor role in females than in males, and T levels are considerably lower in the former, future research is needed to corroborate whether hormone-personality associations in an intrasexual competitive situation are similar across the sexes (Mehta, Welker, Zilioli, & Carré, 2015). Especially the role of competitiveness would be interesting to investigate in women, who are generally found to be lower on this trait than men, presumably since over human evolution women purportedly competed less for mates and other resources than men did (Owens, 2017). A first study (Hahn, Fisher, Cobey, DeBruine, & Jones, 2016) has shown a positive association between baseline T and self-reported intrasexual competitiveness (*N* = 136 women). It would hence be interesting to examine whether such associations can be replicated involving competition-induced T fluctuations in women. Further studies could investigate effects of competitive interactions in other age groups, such as adolescents, a phase marked by increased aggression and risk-taking. These behaviours would be interesting to examine on a state basis in association with hormonal reactivity (Gray, McHale, & Carré, 2017). Additionally, the effects of hormonal reactivity in intrasexual competition could be studied in older male adults, at an age when T levels declined considerably, compared to early adulthood (Keevil et al., 2017). A particularly interesting sample to disentangle age and relationship status effects on the results we found could be middle-aged and older men that transitioned from stable romantic relationships back to singlehood, as re-entering the mating market should shift their life history priorities back from parental and nurturing effort to mating and status competition. Since our findings are based on a western sample mainly from the student population, replications in non-student samples as well as different, non-western cultures are necessary, the latter to assess cross-cultural consistency of our findings. For example, previous research showed intercultural differences in baseline T (Bribiescas, 1998), potentially due to variation in men's reproductive effort (Alvergne, Faurie, & Raymond, 2009).

Moreover, for an evolutionarily complete account of the association between hormonal reactivity and personality variability in an intrasexually competitive context, one needs to take into account further levels of analysis, besides the overly proximate mechanisms considered in the present article (Simpson, Griskevicius, & Kim, 2011; Tinbergen, 1963). A longitudinal follow-up study could investigate functional consequences of acute T reactivity and personality state changes, and hence associations with men's mating success and ultimately reproductive fitness (ideally towards the end of men's reproductive period and hence their lifespan; Pollet, Cobey, & van der Meij, 2013). This would provide insights into the adaptiveness and potential adaptation (e.g. informing about mechanisms of sexual selection; Puts, 2016) of extant human individual differences (e.g., Dall, Houston, & McNamara, 2004; Muehlenbein, 2006). Finally, to further elaborate on phylogenetic mechanisms, comparative studies in related species, such as nonhuman primates, are required (Eisenegger, Haushofer, & Fehr, 2011; Fuxjager, Trainor, & Marler, 2017). Testing the challenge hypothesis, several studies have shown

T increases in competitive mating contexts in species such as chimpanzees (Muller & Wrangham, 2004). Ostner, Heistermann, and Schülke (2011) found a positive relationship between aggressiveness and fecal androgens (in particular, immunoreactive epiandrosterone (iEA), a major metabolite of testosterone in macaque feces) in male Assamese macaques over a 16-month period. Further studies could investigate associations between competition-induced changes in T and personality states in nonhuman primate species to shed further light on the phylogeny and evolutionary basis of this study's findings.

A crucial question we could not fully address is that of causality. We detected larger increases in self-reported competitiveness with stronger T reactivity in the experimental group. Since these are correlated changes, it remains unclear whether T reactivity caused these personality state changes (Carré & Olmstead, 2015). It remains possible that the T response did not have any causal influence at all, and the personality change could be ascribed to a third variable. Moreover, this study was not designed to disentangle which particular aspect of the experimentally manipulated context (intrasexual competition, female exposure, or their combination) had the largest impact on state and hormonal changes. To be able to make causal interpretations, one way would be to administer T and subsequently measure its effects on personality states (McCall & Singer, 2012).

Regarding diverging self-reported and observed personality state changes, it would be interesting to analyse more objectively which changes in mimics and gestures mediated observable personality state changes. Objective behaviours such as gaze direction, smiling/laughing, illustrators (communicative gestures) and adaptors (non-illustrative hand movements) (Penke & Asendorpf, 2008) could be coded and analysed in conjunction with personality and hormonal changes. This would provide further insights into how competition-induced personality state changes, partly mediated by T increases, facilitate social signalling.

Geniole, Carré and McCormick (2011) note that hormonal effects may to a large extent depend on contextual factors (e.g., opponent's psychological state such as self-efficacy and dominance; Van der Meij, Buunk, Almela, & Salvador, 2010; social inclusion vs. exclusion, stable vs. unstable hierarchies; Knight & Mehta, 2014), and that these have not been acknowledged sufficiently in the extant literature. Further research on contextual factor is called for, to further examine the robustness of our and previous findings, and the strength of a “winner effect”, if it exists at all. Future studies could explicitly vary the context in which hormone-personality/behaviour interactions are being examined (Gleason, Fuxjager, Oyegbile, & Marler, 2009). The effect of an audience varying in sex ratios and responsivity (Ronay & von Hippel, 2010), the kind of competition (more sportive or mating-related), or men’s behaviour in an actual mating situation could be assessed. In the latter, a group of single males and females interacting freely in an externally valid dating context could be observed in order to study the conjunction of hormonal and personality variables as well as mating outcomes. Such studies would provide further insight into the complex nature of interactions between contextual factors and hormonal associations with behaviour in competitive situations, specifically, and social interactions, more generally (McCall & Singer, 2012).

Conclusion

In this preregistered study, we demonstrated how hormonal and personality state changes co-occurred in men engaging in an intrasexual competition. We showed a T response after the competition, in line with the challenge hypothesis (Archer, 2006), as well as changes in personality states, recognized not only by the men themselves, but also by outside male and female observers. The larger the T reactivity, the higher increases in self-reported competitiveness, as well as observer-perceived dominance and self-assurance were found. Furthermore, as predicted by the dual-hormone hypothesis (Mehta & Josephs, 2010), an interaction between T reactivity and baseline C on self-reported personality state changes in competitiveness and dominance was found. Our results stress the importance of considering T reactivity during social interactions as a key modulator of personality state changes and social behaviour (Carré, Baird-Rowe, & Hariri, 2014). These findings are also in line with previous accounts of T modulating a life history trade-off between mating and parental effort (e.g., Muehlenbein & Bribiescas, 2005; Muller, 2017; Zilioli & Bird, 2017), and with the steroid/peptide theory of social bonds, according to which high T is related to competitive and low T to nurturing behaviours (van Anders, Goldey, & Kuo, 2011). In addition, outside observers were able to detect personality state changes in dominance and self-assurance that co-occurred with T reactivity based on thin slices of men’s behaviour, suggesting that T may indeed be functional in social signalling towards rivals and potential mates (Puts, 2010).

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4. Manuscript 2

The relative importance of intra- and intersexual selection on human male sexually dimorphic traits

The relative importance of intra- and intersexual selection on human male sexually dimorphic traits

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Abstract

Recent evidence suggests that in sexual selection on human males, intrasexual competition plays a larger role than female choice. In a sample of men (*N* = 164), we sought to provide further evidence on the effects of men's physical dominance and sexual attractiveness on mating success and hence in sexual selection. Objective measures and subjective ratings of male sexually dimorphic traits purportedly under sexual selection (height, vocal and facial masculinity, upper body size from 3D scans, physical strength, and baseline testosterone) and observer perceptions of physical dominance and sexual attractiveness based on self-presentation video recordings were assessed and associated with mating success (sociosexual behaviour and number of potential conceptions) in a partly longitudinal design. Results from structural equation models and selection analyses revealed that physical dominance, but not sexual attractiveness, predicted mating success. Physical dominance mediated associations of upper body size, physical strength, as well as vocal and facial physical dominance and attractiveness with mating success. These findings thus suggest a greater importance of intrasexual competition than female choice in human male sexual selection.

Keywords sexual selection, mating success, physical dominance, sexual attractiveness

Introduction

Sexual selection favours traits that aid in competition for mates and has played a considerable role in the development of human sexual dimorphism (Puts, 2016). Mating competition is assumed to have been particularly intense among men, due to men's greater variance in fitness relative to women's, and an operational sex ratio (OSR; ratio of sexually active men to fecund women) that is male biased (Hill, Bailey, & Puts, 2017). Elevated mating and/or reproductive success in men has been associated with a range of sexually dimorphic traits that develop or increase in expression around sexual maturity, such as muscularity, height, and facial and vocal masculinity (Puts, Bailey, & Reno, 2015). These traits and others, such as agonistic behaviour and status-striving, may have evolved to aid in male intrasexual competition for mates, territory and resources (Puts, 2016; Puts, Bailey, & Reno, 2015). Another mechanism of sexual selection is female mate choice (intersexual selection), whereby females choose males as sexual partners based on preferences for males' traits (Puts, 2010). For a long time, female mate choice was assumed to be the primary mechanism of sexual selection driving the evolution of sexually dimorphic traits in men (Saxton, Mackey, McCarty, & Neave, 2016). Recent evidence, however, indicates that intrasexual (i.e., male-male) competition may have played a larger role than female mate choice (Hill, Bailey, & Puts, 2017).

Hill and colleagues (2013) investigated the influence of men's sexual attractiveness to women (as a proxy measure of female choice), physical dominance (indicating male-male competition) and related traits on mating success, and hence their relative importance in sexual selection (*N*=63 men). In particular, they assessed men's facial masculinity (a composite measure based on Penton-Voak & Perrett, 2001) and vocal masculinity (an aggregate of fundamental frequency (F0, the acoustic parameter closest to pitch) and formant frequencies (resonant frequencies that influence perceptions of vocal timbre)), body height, and girth (a composite body measure consisting of upper arm, chest and shoulder girth, and body weight). Hill and colleagues also obtained evaluations of men's sexual attractiveness and physical dominance made by familiar female and male acquaintances, respectively, as well as men's reported number of sexual partners within the previous twelve months. Physical dominance and associated traits (in particular, girth and vocal masculinity), but not attractiveness, significantly and positively predicted mating success. In a further study on highly sexually dimorphic F0, the voice recordings of men (*N*=175) with lower F0 were rated to be more dominant (by males) and more sexually attractive (by females) (Puts et al., 2016). When analyzing both simultaneously, perceived physical dominance but not sexual attractiveness remained significantly associated with F0, again indicating a potentially stronger role of male-male competition than female mate choice. Saxton and colleagues (2016) investigated the effects of men's F0 and beard growth (*N*=6, for each four different beard growth stages and four voice manipulations, overall 96 stimuli) on perceptions of dominance and attractiveness based on video recordings. Masculine (lower) F0 and beard growth positively influenced dominance ratings, whereas the relationship between F0 and attractiveness was negatively curvilinear (i.e., intermediate values were most attractive). The authors interpreted these findings as suggesting context-dependent (intra- or intersexual selection) differential optimum levels of facial hair and F0. Similarly, Dixson and Vasey (2012) showed that men with full beards were judged to be more aggressive and higher in social status, but not more attractive, compared to when completely shaved (*N*=19, within-subject design). Antfolk and colleagues (2015) provided evidence for a role of female mate choice, in that men's sexual activity appeared to be more constrained by women than vice versa. Because no effects of intrasexual competition were estimated, the relative influence of these two mechanisms of sexual selection could not be ascertained from their study.

Overall, these studies suggest a larger influence of male-male competition versus female mate choice in men's sexual selection, yet important questions remain. Prior studies on human sexual selection have been limited in the number of relevant traits investigated, and the role of additional sexually selected traits, such as physical strength, or baseline testosterone (T) as a physiological basis of sexually dimorphic traits, has been largely ignored. Physical strength obviously is an influential trait in male-male contest competition (Sell, Hone, & Pound, 2012), increasing physical dominance and thus potentially augmenting mating success (Hill et al., 2013). T has been proposed to underlie mechanisms facilitating trade-offs between mating and parenting efforts, especially in men (e.g., Muller, 2017; Puts et al., 2015), and has been associated with attractiveness (e.g., Roney et al., 2006; *N*=39 men), dominance (e.g., Dabbs, 1997; *N*=119 men) and mating success (Peters, Simmons, & Rhodes, 2008; *N*=119 men; but see Puts et al., 2015; *N*=61 men). Our study extends previous research by including these sexually dimorphic traits, which may have been central in men's sexual selection, as well as F0, upper body size/girth, and body height. Moreover, in previous studies, sample sizes were rather small (*N*=19 and 63 men, in Dixson & Vasey and Hill et al., respectively), and the samples in Hill and colleagues and Puts and colleagues had very low mean ages and narrow age ranges around 20 years, so that the robustness and generalizability of these findings remain to be investigated.

Hunt, Breuker, Sadowski and Moore (2009) emphasized the importance of assessing the form and strength of both male-male competition and female mate choice, as well as their interaction (i.e., correlational selection) simultaneously, in order to elucidate total sexual selection operating on male phenotypic traits. In addition, the effects of men's traits on attractiveness (e.g., Cunningham & Barbee, 1990; Neave & Shields, 2008; Saxton, Mackey, McCarty, & Neave, 2015), dominance (e.g., Saxton, Mackey, McCarty, & Neave; Wolff & Puts, 2010) and mating or reproductive success (e.g., Stulp, Pollet, Verhulst, & Buunk, 2012) are sometimes nonlinear, calling for an investigation of both linear and quadratic effects (i.e., stabilizing or disruptive selection), as well as the selection that targets the covariance between different traits (i.e., correlational selection).

Our study thus aimed to investigate the relative roles of male-male competition and female mate choice in men's mating competition by adding several study elements. First, we measured additional traits (baseline T, physical strength; Hill, Bailey, & Puts, 2017). Second, we obtained observer ratings of men's vocal, facial and bodily stimuli on sexual attractiveness and physical dominance (Dixson & Vasey, 2012; Hill et al., 2013; Puts et al., 2016). Third, we considered more complete operationalizations of mating success, in addition to men's number of sexual partners within the previous twelve months, as in Hill and colleagues (2013). Specifically, we employed the full and hence more reliable sociosexual behaviour facet (adding the lifetime number of one-night stands and sexual partners without relationship interest; Penke & Asendorpf, 2008). We also estimated the number of conceptions that would likely have resulted from each man's pattern of copulatory behaviour over the past 18 months in the absence of reliable contraception (number of potential conceptions, NPC; Perusse, 1993). This integrated measure, which incorporates data on both a man's number of sexual partners and his number of copulations with each, should more closely reflect a man's expected reproductive success in a natural fertility population, such as those in which humans spent the vast majority of their evolution. Fourth, previous studies have predominantly employed a cross-sectional design, which makes causal interpretations difficult. We also investigated men's mating success assessed 18 months after the initial measurement of their traits. This partly longitudinal design enables us to examine potentially causal predictions of men's mating success by their objectively measured sexually dimorphic traits and subjective impressions on raters. Finally, we examined these relationships in a larger sample spanning a broader age range and from a different population (Germany). We hypothesize that dominance and related traits will more strongly predict men's mating success than attractiveness and associated variables (Hill et al., 2013; Puts et al., 2016). Moreover, we predict that perceived physical dominance, but not rated sexual attractiveness, will mediate the association between both objective traits and subjective ratings, and mating success (Hill et al., 2013).

Methods

Participants. We recruited 165 male heterosexual young adults with no hormonal disorders. One participant was excluded due to indicating a bisexual orientation, leaving a final sample of *N*=164 (age: *M*=24.2, *SD*=3.2, range: 18-34 years). The final sample size had sufficient power (>.80) to detect effect sizes of Pearson's *r*>.21 (Cohen, 1992). Ninety reported being single (including 11 who were in open relationships), 74 in relationships (66 committed, 4 engaged, 4 married), 88.4% were students (of which 2 were psychology students). On the 7-point Kinsey scale of sexual identity (0 = exclusively heterosexual to 6 = exclusively homosexual; Kinsey, Pomeroy, & Martin, 1948), the mean was 0.17 (range 0-2; *SD*=0.41). All procedures received ethics approval from the Georg-Elias-Müller-Institute of Psychology's Ethics Committee (no. 111).

Procedure. For the first assessment (T1), participants visited the lab twice. During the first "pre-session" visit, participants provided informed consent and self-reports on personality traits. In addition, anthropometric measures (3D body and face scans, handgrip and upper body strength, body height and weight) were taken and their sexual history assessed (see below). A first saliva sample was taken approximately 20 minutes after arriving at the lab (to allow participants to calm down), to obtain a first measure of baseline T levels. To control for circadian variation in participants' hormonal levels, all testing was conducted between 2pm and 6pm (Idris, Wan, Zhang, & Punyadeera, 2017; Schultheiss & Stanton, 2009). During the second "main session" visit a few days after the pre-session, participants provided a second saliva sample for baseline T measures 12-15 minutes after arriving at the lab. Afterwards, they were escorted into the video laboratory to complete video recordings (one-minute recordings of participants talking about their personal strengths; see below). Participants subsequently engaged in further tasks not relevant to this study (see Kordsmeyer & Penke, 2017). At the end of the main session, participants were debriefed about the study's objective.

Hormonal assessment. For both samples, participants provided at least 2 ml of saliva via unstimulated passive drool through a straw (Schultheiss, Schiepe, & Rawolle, 2012; Fiers et al., 2014). The samples were immediately transported to an ultra-low temperature freezer (-80°C), where salivary T is stable for at least 36 months (Granger, Shirtcliff, Booth, Kivlighan, & Schwartz, 2004). At the end of data collection, saliva samples were shipped on dry ice to the Technical University of Dresden, where they were analyzed using chemiluminescence immunoassays with high sensitivity (IBL International, Hamburg, Germany). The intra- and inter-assay coefficients (CVs) for T are below 11 %. Outliers were winsorized to 3 SDs (n=9, in accordance with Mehta, Welker, Zilioli, & Carre, 2015; see also Pollet & van der Meij (2017) for an extensive discussion of the influence of hormone outlier handling on significance testing). T values appeared to be positively skewed and to violate the assumption of normality (Shapiro-Wilk test W<.96, ps<.001). Consequently, both baseline T variables were log10-transformed (e.g., Mehta, Welker, Zilioli, & Carré, 2015). One participant had missing data for baseline T (decreasing the sample size for analyses involving this measure to N=163). Participants were asked to refrain from drinking alcohol, exercising, and taking recreational or non-prescribed clinical drugs on both days of the study; ingesting caffeine (coffee, tea, coke) or sleeping three hours before; and from eating, drinking (except for water), smoking or brushing teeth one hour before their scheduled appointment (Geniole, Busseri, & McCormick, 2013; Lopez, Hay, & Conklin, 2009). To check participants' adherence to these instructions and to assess further potential influences on the saliva samples and hormonal levels, a screening questionnaire was administered at the beginning of the session (Schultheiss & Stanton, 2009). None of the 163 participants indicated taking hormonal medication or supplements. Saliva samples were immediately controlled for blood traces and measures were repeated if necessary. Independent from this, 38 participants reported either recent gum bleedings or oral infections, which can lead to elevated steroid hormone concentrations (Schultheiss & Stanton, 2009). Baseline T levels were compared for these as a group with the remaining participants and no differences were detected (all ts<0.44, ps>.66). Finally, both T values were aggregated to form a more reliable measure of baseline T (Idris, Wan, Zhang, & Punyadeera, 2017).

Video recordings. Each participant was first told that the question he should answer while being videotaped within a one-minute time limit was, "What do you think right now, is great about yourself?". Then he was presented with one of two sets of eight terms about "life domains" (e.g., "humour" and "friendship"; Table S1) and instructed to choose three, which he would subsequently talk about. The participants were given these terms as hints for what to talk about and in order to ensure that they talked about a variety of different, but roughly comparable topics when presenting themselves. The three chosen domains were placed next to the camera, with the participant standing approximately four meters away from the camera (to have a full-body view). Participants could start speaking whenever they wished and were gently notified when they passed the time limit, but not stopped abruptly.

Anthropometric measures. Participants were scanned three times during the pre-session using a Vitus Smart XXL 3D bodyscanner, running AnthroScan software (both Human Solutions GmbH, Kaiserslautern, Germany), while wearing tight underwear. Participants were instructed to stand upright with legs hip-width apart, arms extended and held slightly away from the body, making a fist with thumbs showing forward, the head positioned in accordance with the Frankfort Horizontal, and to breathe normally during the scanning process. Participants were asked to directly face the camera and show a neutral facial expression while two photos were taken of each participant's face in front of a white wall. The more suitable of the two photos (in terms of neutral facial expression and head angle) was chosen for the rating study (see below). Physical strength was operationalized as the average of upper body and handgrip strength. Both were measured using a hand dynamometer (Saehan SH5001). Each measurement was taken three times, starting with handgrip strength, for which participants were asked to use their dominant hand (88.2% used their right). Upper body strength was measured with the dynamometer following the procedure described in Sell, Cosmides, Tooby, Sznycer, von Rueden and Gurven (2009). A composite strength measure was formed by averaging the maximum values for each of the three measures of handgrip and upper body strength. Body height (in cm) was measured twice using a stadiometer while participants stood barefoot, and the two values were averaged. An aggregate indicator of upper body size (Price, Dunn, Hopkins, & Kang, 2012) was calculated by averaging *z*-standardized shoulder width, bust-chest girth, and upper arm girth (means of left and right arms), based on averages of automatic measurements extracted from the three body scans (measures according to ISO 20685:200). Reliabilities for the three body scans were high for all measures (ICCs>.90). To obtain fundamental frequency (F0) measurements, sound clips were extracted from the self-presentation video recordings (for which Line6 XD-V75 microphones were used) and cut to a length of five seconds, beginning five seconds after the male participants started to speak. Sound files were analyzed as described in Study 2 of Puts et al. (2016) using PRAAT software (v. 6.0.14).

Sexual history. Men reported their sociosexual orientation (SOI-R; Penke & Asendorpf, 2008). Mating success was conceptualized as the behaviour facet of the SOI-R inventory, i.e., an aggregate of participants' number of sexual partners within the last twelve months, lifetime number of one-night stands and of sexual partners without relationship interest. In order to replicate the findings of Hill and colleagues (2013), results with only the first item of the SOI-R scale (i.e., participants' number of sexual partners within the last 12 months) are reported also.

Video ratings. For proxy measures of male-male competition and female mate choice, men's self-presentation video recordings were rated for physical dominance (by males, "How likely is it that this man would win a physical fight with another man?", using an 11-point Likert-scale, from -5="extremely unlikely" to +5="extremely likely") and sexual attractiveness (by females, "How sexually attractive is this man?", using an 11-point Likert-scale, from -5="extremely unattractive" to +5="extremely attractive"). We assessed perceptions of sexual attractiveness, rather than attractiveness for a long-term, committed relationship because men's masculine traits should be more strongly related to the former (Frederick & Haselton, 2007), and because we expected sexual attractiveness to more strongly influence sexual outcomes, such as number of sexual partners. One hundred and sixty raters (80 females; age: *M*=24.1, *SD*=6.1, range 18-63 years) were recruited from the local participant pool. The video stimuli were divided into eight sets, and each video was rated by ten independent female (for sexual attractiveness) and male (for physical dominance) raters. Because some target men exceeded the time limit of one minute, all videos were cut to a maximum length of one minute. The videos of seven participants were removed from the stimulus sample due to audio problems, leaving a final set of *N*=157 target men. Interrater agreements were high (Cronbach's α>.85).

Additional ratings. In order to obtain further information on men's traits not captured by the objective trait measurements described above, naive observers provided judgments of physical dominance and sexual attractiveness based on men's bodies, faces and voices. For bodily attractiveness and dominance ratings based on target men's 3D body scans, 44 participants (21 females; age *M*=22.9, *SD*=5.7, range 18-48 years) were recruited from the local participant pool. The 3D body scans of 13 target men had to be removed due to errors with the scans, leaving a final stimulus set of *N*=151 body scans. From each of the target men, one body scan was chosen by visual inspection (i.e., the scan coming closest to the standard posture). Body scans were truncated above the neck using the software Blender (version 2.75, www.blender.org), leaving an even plane just below the larynx. This was done in order to focus raters' attention on bodily features and to preserve anonymity of male participants. Animated videos of a body scan turning around its vertical axis ("beauty turns", duration: 8 sec. each; 960x540 pixels) were created. The 151 beauty turns were divided into two sets of 76 and 75 videos matched for BMI. After previewing all beauty turns (1 sec. each) to familiarize the raters with the stimulus material and range of bodies, ratings were conducted with the beauty turns being displayed in random order on 24" computer screens. Physical dominance and sexual attractiveness were assessed as with video ratings above. Each set of beauty turns was rated by 10-13 males and females each. Interrater reliabilities within each set and rater sex were high (Cronbach's α>.91). For voice ratings, 60 participants (30 females; age: *M*=19.7, *SD* 4.0, range 18-48 years) were recruited at an US-American university. Raters provided information on their German language knowledge, which indicated that most raters had no comprehension of German language, ensuring our voice ratings were unbiased by spoken content. The five-second voice recordings (as described above) were played to raters using Sennheiser HD 280 Professional headphones. Overall each voice recording was judged by 15 male raters on physical dominance and 15 female raters on sexual attractiveness (mean ratings were used). Physical dominance was rated using the item "How likely is it that this man would win a physical fight against another man?" on a 7-point Likert scale, with the endpoints 1="very unlikely" to 7="very likely". Sexual attractiveness was rated using the item "How sexually attractive is this man?" on a 7-point Likert scale, with the endpoints 1="very unattractive" to 7="very attractive". Interrater reliabilities for both items were good (Cronbach's α>.80). Facial ratings were conducted on target men's facial photographs (frontal photos, with a neutral facial expression) by 23 independent raters (11 males; age: *M*=27.3, *SD*=8.8, range 19-54 years). Males rated physical dominance using the item "How likely is it that this man would win a physical fight against another man?" on an 11-point Likert scale, with the endpoints -5="very unlikely" to +5="very likely". Females rated sexual attractiveness using the item "How sexually attractive is this man?" on an 11-point Likert scale, with the endpoints -5="extremely unattractive" to +5="extremely attractive". Interrater reliabilities were good (Cronbach's α>.82). Fourteen data points from 14 raters who indicated that they knew a given target man well were excluded from subsequent analyses.

Follow-up study. Exactly 18 months after T1, participants were invited to fill in an online questionnaire (T2), assessing their sexual history since the first study (using formr.org; Arslan & Tata, 2017). One hundred and nine participants (66.5 %) completed the questionnaire (age: *M*=25.8, *SD*=3.2 years). Corresponding to T1, mating success was conceptualized as the behaviour facet of the SOI-R. In addition, the number of potential conceptions (NPCs) were calculated according to the following formula by Perusse (1993), taking into account the number of (female) sexual partners within the last 18 months, the number of instances of vaginal intercourse (as indicated on a 9-point scale: 0, 1, 2, 3, 4, 5 to 6, 7 to 9, 10 to 19, 20 or more times), and a fixed estimated probability of conception for each sexual act (3%), yielding an estimate of number of conceptions (i.e., fertilized ova) that would have resulted if mating had occurred randomly across the ovulatory cycle and in the absence of contraception (see also Linton & Wiener, 2001):

$$\mathrm{NPC} = \sum_{m=1}^{n} (1 - 0.97^{P_m})$$

where n is the number of sexual partners, and P_m the number of coital acts with partner m. We chose to include the measure of NPCs, as it partially corrects for a confound of a simple measure of numbers of sexual partners: highly attractive or dominant men may eventually achieve a high reproductive fitness with one romantic partner, but this is not reflected in the recent number of sexual partners (especially in light of socially imposed norms of monogamy; Perusse, 1993), whereas less attractive or dominant men who are single may have had a few more recent sexual partners (e.g., one-night stands), but in the end achieve a lower reproductive fitness. The NPCs adjusts for this by taking into account the number of copulations with each partner, which should be large for men in stable romantic relationships, compared to short-term sexual encounters. Finally, in line with T1 and to replicate Hill and colleagues' findings (2013), results with only the first item of the SOI-R inventory are reported as well.

Statistical analyses. To obtain relative fitness measures, the mating outcome variables (SOI-R items 1-3, NPCs) were divided by the sample mean (Hill et al., 2013). Trait measures and mean subjective ratings were *z*-standardized. Structural equation models were conducted to examine to what extent men's sexually dimorphic traits and observer impressions of their physical dominance and sexual attractiveness were associated with mating success. For these, the *lavaan* package in R (R Core Team, 2015; Rosseel, 2012) was used, including objective trait measures and subjective ratings (in separate models), video-rated physical dominance and sexual attractiveness, as well as mating success (T1 & T2: SOI-R items 1-3 loading on a latent factor sociosexual behaviour, SOI-R item 1; T2 only: NPCs; Fig. 1 and 2). Because all SOI-R items 1-3 and the NPC variable were positively skewed (Shapiro-Wilk test: $W<.87$, $p<.001$), maximum likelihood estimation with robust (Huber-White) standard errors (MLR) was used (except for the Vuong test reported below, for which regular maximum likelihood estimation is required). Quadratic effects were included by squaring the trait and rating measures. To find the model best fitting the data, we ran model comparisons employing the Scaled Chi-Square Difference Test (Satorra & Bentler, 2001) for nested models, and the Vuong test and calculated confidence intervals for BIC differences for non-nested models (R package *nonnest2*; Merkle, You, & Preacher, 2016; Vuong, 1989). Mediator analyses were conducted using the lavaan package in R. For robustness checks, we added men's relationship status (binary, single including "open relationship" vs. partnered; Linton & Wiener, 2001) and age (Thornhill & Gangestad, 1994) to the structural equation models.

The T2 measure of sociosexual behaviour partly overlaps with its T1 assessment (items 2 and 3 ask for the lifetime number of one-night stands and sexual partners without relationship interest; also evidenced by the correlation between T1 and T2, $r=.80$). This is not the case for the first item on the number of sexual partners within the previous twelve months, as it was assessed 18 months after T1. Due to the considerably larger sample size and consequently higher power at T1 ($N=164$; T2 $n=109$), we decided to focus on sociosexual behaviour at T1 for further selection analyses (selection gradients and canonical analyses).

Selection analyses. Multivariate selection analysis (Lande & Arnold, 1983) was used to formally quantify the linear and nonlinear (i.e., quadratic and correlational selection) selection on men's traits. We applied a linear transformation to the variables rated physical dominance and sexual attractiveness (ranging from -5 to +5), adding a constant of five to each value, to avoid negative values, as differences in scale are known to alter estimated gradients in selection analyses (Brodie & Janzen, 1996). We employed two separate multiple regression models: the first to estimate standardized linear selection gradients (β), and the second to calculate quadratic and cross-product terms to estimate the matrix of standardized nonlinear selection gradients (γ) (Phillips & Arnold, 1989). Since interpreting individual effects in γ can underestimate the actual strength of sexual selection (Blows & Brooks, 2003), we performed canonical analyses of the γ matrix to find the major axes of the response surface, resulting in an M matrix with i eigenvectors (m_i; where i is the number of traits), each describing a major axis of the response surface. The strength of linear selection along each eigenvector is indicated by Θi, and the strength of nonlinear selection by its eigenvalue (λi) (Phillips & Arnold, 1989). We estimated Θi using the double linear regression method (Bisgaard & Ankenman, 1996) and λi using the permutation procedure of Reynolds, Childers, and Pajewski (2010). As our response variables were not normally distributed, we tested the significance of our standardized selection gradients and linear and nonlinear selection operating on the eigenvectors of γ using randomization tests (Lewis, Wedell, & Hunt, 2011; Mitchell-Olds & Shaw; 1987). Major axes of the response surface extracted from the canonical analyses of γ were visualized using thin plate splines when two or more axes showed statistically significant nonlinear selection (Green & Silverman, 1994). The response surface was created using the lambda value that minimized the generalized cross-validation (GCV) score was fit employing the *Tps* function in the *fields* package of R (version 3.2.2). When significant selection only targeted a single axis, we visualized this using a univariate spline emplyoing the *splines* package in R. A sequential model-building approach was used to compare mechanisms of sexual selection to each other and to mating success (Draper & John, 1988). A hierarchical model was run to first compare linear sexual selection, then quadratic and correlational sexual selection to identify whether the direction and form of sexual selection on male traits differ across these episodes. To determine which individual traits contributed to any overall significant difference, univariate interaction terms from the complete models were used (Lewis, Wedell, & Hunt, 2011).

Data availability. The data and analysis scripts associated with this research are available at osf.io/z4dxa.

Results

Preliminary Analyses.

Descriptive statistics for all measured variables and bivariate Pearson correlations between all main variables can be found in the online supplementary material (Tables S2 and S3).

Structural equation models and mediation analyses.

Model selection. We compared different structural equation models (SEMs) in order to find out which model fit our data best. First, we built a complete model including linear and quadratic effects (on video-rated physical dominance and sexual attractiveness, and on mating success), as well as direct effects of the five objective traits and six subjective ratings on each of the mating success variables separately (corresponding to Hill et al., 2013; see Fig. 1 and 2). As video-rated dominance and attractiveness were substantially correlated (for both T1/T2 samples: *r*s=.55, *p*s<.001, *N*=164/107), possibly due to halo effects, we included the covariance between these two as a next step. Model comparison (nested models, Scaled Chi-Square Difference Test; Satorra & Bentler, 2001) showed a clearly better fit of the latter model including the covariance (for model comparison statistics see Tables 1 and S4). Even though the effects of objective traits and subjective ratings may be mediated by perceived attractiveness and dominance, Hill and colleagues (2013) showed direct effects of objective traits (girth) on mating success. We analyzed whether model fit would significantly improve when removing these direct effects and it did (at least for objective traits; Tables 1 and S4). As previous studies showed quadratic effects on mating success (Hill et al., 2013; Saxton, Mackey, McCarty, & Neave, 2015), we examined if model fit would improve when retaining these terms. Model comparison showed that model fit improved significantly when excluding quadratic effects on rated dominance and attractiveness, and on mating success. However, previous research has shown that there may still be quadratic effects of men's traits on either sexual attractiveness or physical dominance, but not both (e.g., Saxton et al., 2015 found nonlinear associations of fundamental frequency (F0) with attractiveness, but only linear effects on dominance; Hill et al., 2013 found a positive quadratic effect of facial masculinity on rated physical dominance). Thus, we additionally tested models including quadratic effects of objective traits and subjective ratings on either video-rated dominance or attractiveness in two separate models. Results showed that model fit was significantly better excluding any quadratic effects (Table 1). The models with the best fit overall are shown in Fig. 1 and 2 (mating success measured as sociosexual behaviour at T1).

Table 1

Structural equation model comparison statistics for different versions of model 1.

Nested model comparisons	χ^2 difference	*p*	Result			
Full model: include covariance between sexual attractiveness and physical dominance?	25.58	<.001	better fit including covariance			
Include "long paths" (direct effects of traits on mating success)?	35.34	<.001	better fit excluding "long paths"			
Non-nested model comparisons	Vuong test		AIC difference		BIC difference	
	z	*p*	*CI lower*	*CI upper*	*CI lower*	*CI upper*
Include quadratic besides linear effects?	-37.11 → exclude	<.001	3749.87	4165.42	3787.06	4202.61
Full model vs. excluding long paths & quadratic effects	-38.05 → exclude	<.001	3744.39	4146.29	3812.58	4214.49
Include quadratic effects on sexual attractiveness only?	29.97 → exclude	<.001	-3186.57	-2796.58	-3202.07	-2812.08
Include quadratic effects on physical dominance?	30.04 → exclude	<.001	3187.41	-2798.18	-3202.90	-2813.69

Note: sociosexual behaviour at T1 as outcome, objective traits as predictors; χ^2 = chi-square; AIC = Akaike information criterion; BIC = Bayesian information criterion; CI = confidence interval; lower/upper = lower/upper bound.

Table 2

Fit statistics of all ten final structural equation models.

Predictors	Outcome	χ^2	*p*	*CFI*	*TLI*	*RMSEA*
Objective traits	Sociosexual behaviour T1	26.23	.12	0.98	0.96	.059
Subjective ratings	Sociosexual behaviour T1	28.98	.15	0.99	0.97	.045
Objective traits	Sexual partners 12 months T1	9.20	.10	0.96	0.86	.073
Subjective ratings	Sexual partners 12 months T1	8.08	.23	0.99	0.97	.046
Objective traits	Sociosexual behaviour T2	16.01	.66	1.00	1.02	.000
Subjective ratings	Sociosexual behaviour T2	20.39	.56	1.00	1.01	.000
Objective traits	Sexual partners 12 months T2	7.11	.21	0.97	0.90	.060
Subjective ratings	Sexual partners 12 months T2	4.81	.57	1.00	1.03	.000
Objective traits	NPCs T2	3.65	.60	1.00	1.07	.000
Subjective ratings	NPCs T2	4.36	.63	1.00	1.05	.000

Note: T1/T2 = time point 1/2; NPCs = number of potential conceptions; χ^2 = chi-square; *CFI* = robust Comparative Fit Index; *TLI* = robust Tucker-Lewis Index; RMSEA = robust Root Mean Square Error of Approximation.

Model 1: sociosexual behaviour at T1 as outcome, objective traits as predictors. Results of this final model revealed a negative effect of F0 and a positive effect of physical strength on video-rated sexual attractiveness, and positive effects of upper body size and physical strength, as well as a negative effect of F0 on rated physical dominance (Fig. 1). Video-rated physical dominance positively predicted sociosexual behaviour, and mediated associations of upper body size and physical strength with mating success (Table 3; all unsigned indirect effects for video-rated sexual attractiveness <.01, *p*s>.13). Results were virtually identical with no changes in significance of effects when including participants' age and relationship status (Fig. S1).

Model 2: sociosexual behaviour at T1 as outcome, subjective ratings as predictors. Results of this final model showed positive effects of rated facial and bodily sexual attractiveness and facial physical dominance on video-rated sexual attractiveness (Fig. 2). Facial sexual attractiveness, vocal, facial and bodily physical dominance were positively related to video-rated physical dominance. Rated physical dominance was positively associated with sociosexual behaviour. Moreover, video-rated physical dominance mediated associations of vocal and facial physical dominance as well as vocal and facial attractiveness with mating success (Table S5). Video-rated sexual attractiveness mediated the association between bodily sexual attractiveness and mating success (Table S6). Results were virtually identical with no changes in significance when including age and relationship status (Fig. S2).

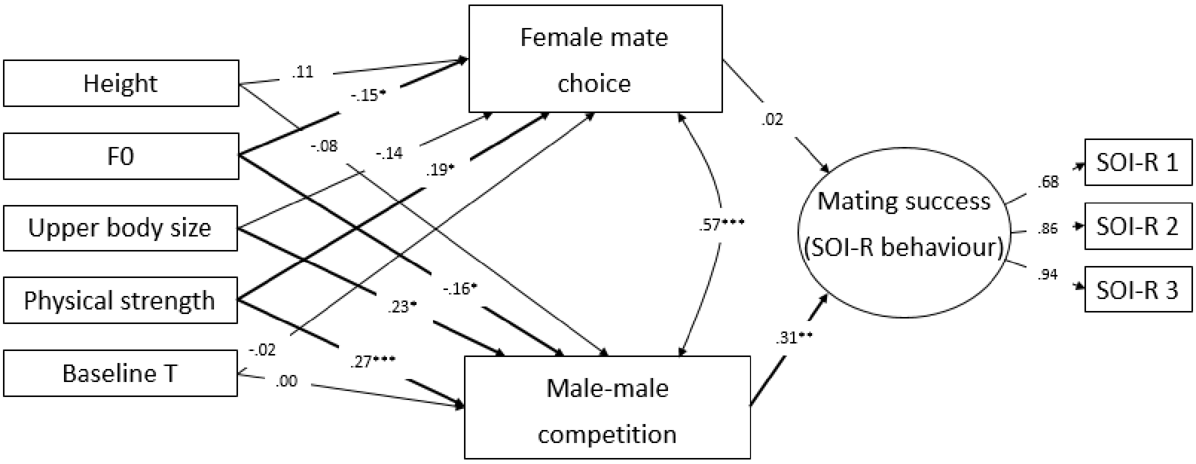

Fig. 1. Structural equation model 1, sociosexual behaviour (SOI-R behaviour) at T1 as outcome and objective traits as predictors; baseline T = baseline testosterone; F0 = fundamental frequency; SOI-R 1/2/3 = items 1/2/3 of the sociosexual orientation inventory; for model fit statistics see Table 2; **p*<.05, ***p*<.01, ****p*<.001.

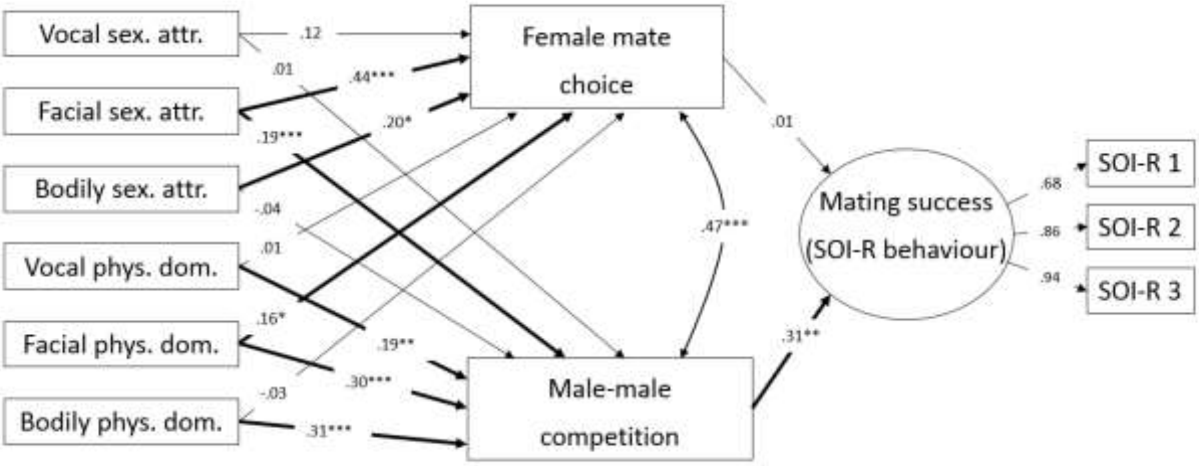

Fig. 2. Structural equation model 2, sociosexual behaviour (SOI-R behaviour) at T1 as outcome and subjective ratings as predictors. Sex. attr. = sexual attractiveness; phys. dom. = physical dominance; SOI-R 1/2/3 = items 1/2/3 of the revised sociosexual orientation inventory; for model fit statistics see Table 2; **p*<.05, ***p*<.01, ****p*<.001.

Models 3 and 4: number of sexual partners during last twelve months at T1 as outcome, objective traits or subjective ratings as predictors. To replicate findings of Hill and colleagues (2013), we applied the number of sexual partners in previous 12 months as the mating success measure. Results were virtually identical to models 1 and 2 with no changes in effects (Fig. S3 and S4), also when including age and relationship status (Fig. S5 and S6).

Models 5 and 6: sociosexual behaviour at T2 as outcome, objective traits or subjective ratings as predictors. For a quasi-longitudinal design predicting men's mating success, we assessed men's number of sexual partners in the twelve months before T2, their lifetime number of one-night stands and sexual partners without relationship interest (thus having some overlap with sociosexual behaviour at T1 for the latter two items; sociosexual behaviour at T1 and T2 correlated r=.80, p<.001). We replicated effects of models 1 and 2 of video-rated physical dominance, but not sexual attractiveness, on sociosexual behaviour (for details and for effects of objective traits/subjective ratings, see Fig. S7 and S8). Results were unchanged when including age and relationship status (Fig. S9 and S10).

Models 7 and 8: number of sexual partners in twelve months at T2 as outcome and objective traits or subjective ratings as predictors. For an actual longitudinal design, we employed men's number of sexual partners in the twelve months previous to T2 as the dependent variable. No effects of video-rated physical dominance or sexual attractiveness were found, either in the model including objective traits or when including subjective ratings (all unsigned *ß*s<.17, *p*s>.08; for details and for effects of objective traits/subjective ratings, see Fig. S11 and S12). Again, results were unchanged when including age and relationship status (Fig. S13 and S14).

Models 9 and 10: number of potential conceptions (NPCs) at T2 as outcome and objective traits or subjective ratings as predictors. Alternatively using NPCs at T2 as the mating success outcome revealed no effects of video-rated physical dominance or sexual attractiveness (all unsigned *ß*s<.18, *ps*>.11; for details and for effects of objective traits/subjective ratings, see Fig. S15 and S16). Results were virtually unchanged when including age and relationship status (Fig. S17 and S18).

Table 3

Mediation analyses for association between objective trait and sociosexual behaviour (T1), mediator: video-rated physical dominance.

Independent variable:	Indirect effect	*SE*	*CI lower*	*CI upper*	*z*
Height	.01	.01	-.01	.03	0.71
Fundamental frequency (F0)	-.02	.01	-.04	.003	-1.73
Upper body size	.03	.01	.001	.06	2.06*
Physical strength	.04	.01	.01	.06	2.49*
Baseline T	.004	.01	-.01	.02	0.51

Note: SE = standard error; CI = confidence interval; **p*<.05.

Selection analysis with objective traits as predictors.

To further examine linear and nonlinear, we employed selection gradient and canonical analyses. We focussed on the outcome variable sociosexual behaviour at T1, as explained above.

Female mate choice. Female choice exerted directional (linear) selection favouring physical strength (Table 4A). There was also significant stabilizing (negative quadratic) selection on upper body size (Table 4A), but no significant correlational selection (Table 4A). Canonical analysis of selection gradients γ revealed one eigenvector with significant negative nonlinear sexual selection (m_5, Table 5A), indicative of stabilizing selection. It was heavily weighted by a negative loading from upper body size (Table 5A; Fig. 3A, in line with regression analyses; Table 4A). This eigenvector was also subject to significant negative linear selection (Table 5A). In addition, there was significant negative linear selection on m_2, facilitating increased physical strength and body height (due to the negative contribution of these traits to this eigenvector; Table 5A).

Male-male competition. Male-male competition exerted directional selection favouring increased upper body size and physical strength (Table 4B). There was also significant disruptive (positive quadratic) selection on body height and stabilizing (negative quadratic) selection on upper body size (Table 4B), as well as negative correlational selection between physical strength and body height, and positive correlational selection between physical strength and F0 (Table 4B): as physical strength increased, shorter men and those with higher voices were perceived as more physically dominant. Canonical analysis of γ revealed two eigenvectors with significant nonlinear sexual selection (m_1 and m_5, Table 5B). The first eigenvector of nonlinear selection (m_1) had a positive eigenvalue (indicative of disruptive selection) and was heavily weighted by a positive loading from body height and a negative loading from physical strength (Table 5B). This eigenvector was also subject to significant negative linear selection, favouring decreased body height and increased physical strength (Table 5B). This result parallels results of the regression analysis in that it signifies negative correlational selection between height and physical strength. The second eigenvector of nonlinear selection (m_5) had a negative eigenvalue (indicative of stabilizing selection) and was heavily weighted by upper body size (Table 5B). There was also significant positive linear selection on m_4, selecting for increased upper body size, physical strength and decreased baseline T (Table 5B). The combination of significant positive and negative eigenvalues suggests that the fitness surface for male-male competition is best described as a multivariate saddle (Fig. 3B).

Table 4

The vector of standardized linear selection gradients (*β*) and the matrix of standardized quadratic and correlational selection gradients (*γ*) for body height, fundamental frequency (F0), upper body size, physical strength and baseline testosterone (T) operating through female choice, male-male competitions and mating success (sociosexual behaviour at time point 1).

	β	***γ***				
		Height	F0	Body size	Phys. str.	T
A. Female choice						
Height	.03 (.03)	-.02 (.06)				
F0	-.06 (.03)	.01 (.04)	-.02 (.04)			
Body size	-.07 (.04)	.04 (.05)	-.04 (.04)	**-.22* (.08)**		
Phys. str.	**.09* (.04)**	.00 (.04)	.03 (.04)	.02 (.06)	.02 (.06)	
T	-.01 (.03)	-.01 (.04)	-.04 (.03)	.03 (.05)	-.03 (.04)	.04 (.06)
B. Male-male competition						
Height	-.03 (.03)	**.12* (.04)**				
F0	-.05 (.03)	.03 (.03)	.02 (.04)			
Body size	**.09* (.03)**	-.00 (.04)	-.08 (.04)	**-.14* (.06)**		
Phys. str.	**.10* (.03)**	**-.08* (.03)**	**.07* (.04)**	.04 (.05)	.02 (.04)	
T	-.00 (.03)	.02 (.03)	-.04 (.03)	.01 (.04)	-.00 (.03)	.01 (.04)
C. Mating success						
Height	-.02 (.05)	-.10 (.08)				
F0	-.06 (.05)	.05 (.06)	.12 (.06)			
Body size	**.17* (.06)**	.06 (.07)	.09 (.06)	-.12 (.10)		
Phys. str.	.06 (.05)	.01 (.06)	.02 (.06)	.03 (.09)	.10 (.08)	
T	.06 (.05)	.04 (.06)	-.05 (.05)	.02 (.07)	-.06 (.06)	-.06 (.08)

Note: Randomization tests: **p*<.05.

Table 5

The M matrix of eigenvectors from the canonical analysis of γ in Table 4 for female choice, male-male competitions and mating success (sociosexual behaviour at T1).

	M					**Selection**	
	Height	F0	Body size	Phys. str.	T	$\boldsymbol{\Theta_i}$	$\boldsymbol{\lambda_i}$
A. Female choice							
$\boldsymbol{m_1}$	.07	.42	-.09	.44	-.79	.03	.09
$\boldsymbol{m_2}$	-.49	.13	-.24	-.74	-.37	**-.07***	-.00
$\boldsymbol{m_3}$	.83	-.11	.09	-.47	-.26	-.01	-.01
$\boldsymbol{m_4}$	.18	.88	-.11	-.14	.41	-.05	-.04
$\boldsymbol{m_5}$	.18	-.18	-.96	.12	.09	**.10***	**-.25***
B. Male-male competition							
$\boldsymbol{m_1}$	.85	-.06	-.07	-.51	.12	**-.08***	**.17***
$\boldsymbol{m_2}$	-.28	-.82	.24	-.32	.31	.04	.09
$\boldsymbol{m_3}$	.21	.08	.16	.52	.81	**.05***	.01
$\boldsymbol{m_4}$	.38	-.37	.49	.50	-.48	**.10***	-.05
$\boldsymbol{m_5}$	.12	-.43	-.82	.35	-.04	-.02	**-.19***
C. Mating success							
$\boldsymbol{m_1}$	.18	.77	.30	.49	-.22	.02	.18
$\boldsymbol{m_2}$	-.15	-.49	-.14	.83	-.19	.05	.10
$\boldsymbol{m_3}$	.52	-.17	.33	.22	.74	**.11***	-.03
$\boldsymbol{m_4}$	-.69	.31	-.21	.16	.60	.01	-.15
$\boldsymbol{m_5}$	.45	.21	-.86	.08	.09	**-.16***	-.18

Note: The linear (Θi) and quadratic (λi) gradients of selection along each eigenvector are given in the last two columns. The quadratic selection gradients (λi) of each eigenvector (m_i) are equivalent to the eigenvalue. Randomization tests: *p<.05.

Female mate choice vs. male-male competition. The strength and form of linear sexual selection acting on the five male traits differed significantly between female choice and male-male competition ($F_{5,300}$=2.60, p=.03; Table 6). This was due to selection for greater upper body size through male-male competition ($F_{1,300}$=9.78, p<.01). There was no difference in quadratic ($F_{5,290}$=1.21, p=.30) or correlational ($F_{10,270}$=0.61, p=.81; Table 6) sexual selection.

Table 6

Hierarchical sequential model comparing sexual selection through male-male competitions versus female choice.

	SS_R	SS_C	Df_1	Df_2	F	p
Linear	40.06	38.39	5	300	2.60	.03^A
Quadratic	35.74	35.01	5	290	1.21	.30
Correlational	33.25	32.52	10	270	0.61	.81

Note: ^{A}Contribution of individual traits: upper body size: $F_{1,300}$=9.78, p<.01; body height: $F_{1,300}$=2.30, p=.13; F0: $F_{1,300}$=0.04, p=.85; physical strength: $F_{1,300}$=0.11, p=.74; baseline testosterone: $F_{1,300}$=0.02, p=.88.

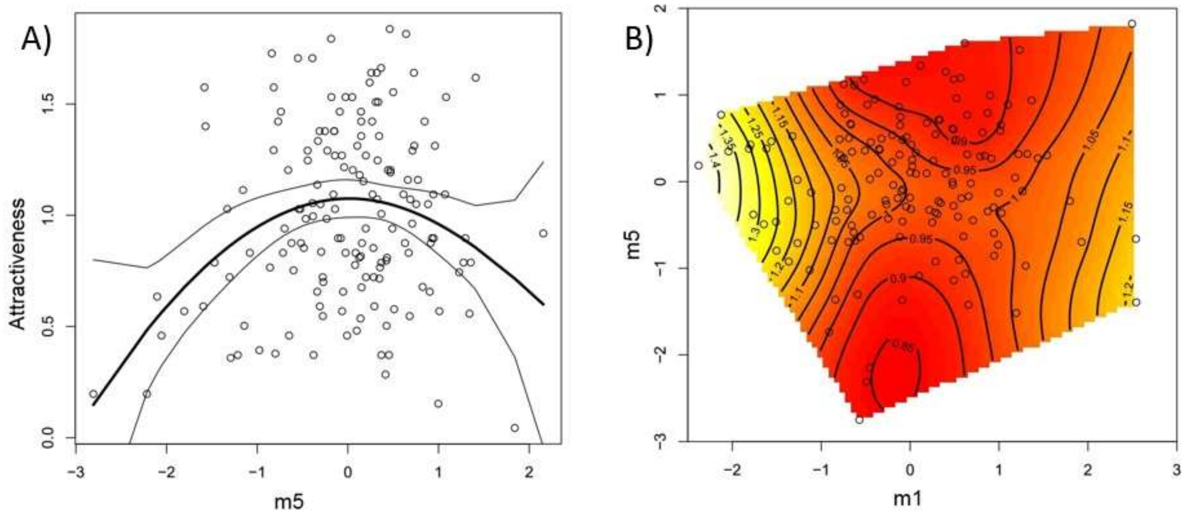

Fig. 3. A) Spline surface, showing quadratic selection for m_5 under female choice (see Table 5A); B) correlational selection on eigenvectors m_1 and m_5 under male-male competition (see Table 5B).

Mating success. Mating success (sociosexual behaviour) exerted directional selection favouring an increased upper body size, but no stabilizing, disruptive or correlational selection (Table 4C). Canonical analysis of γ revealed two eigenvectors with significant linear sexual selection (m_3 and m_5; Table 5C), which favoured increased body height and baseline T (m_3) as well as increased upper body size and decreased body height (m_5; due to negative and positive contributions of these traits to the negative eigenvectors, respectively; Table 5C). No significant nonlinear selection was detected (Table 5C).

When mating success was used as the fitness measure and video-rated sexual attractiveness (as a proxy of male-male competition) and video-rated physical dominance (as an indicator of female choice) were treated as traits, there was directional selection for success in male-male competition, but not female mate choice (Table 7). Canonical analysis revealed one significant eigenvector with significant linear selection (m_1), favouring both male-male competitions and female choice (due to negative contributions to the negative eigenvector; Table 8), of which male-male competition showed a slightly greater weight. No significant nonlinear selection was detected (Table 8).

Table 7

The vector of standardized linear selection gradients (*β*) and the matrix of standardized quadratic and correlational selection gradients (*γ*) for female choice and male-male competitions operating through mating success (sociosexual behaviour at T1).

	β	***γ***	
		Male comp.	Fem. choice
Mating success			
Male comp.	**.19* (.06)**	.03 (.10)	
Fem. choice	.01 (.06)	.07 (.08)	-.01 (.10)

Note: Male comp. = male-male competition; fem. choice = female choice; randomization tests: **p*<.05.

Table 8

The M matrix of eigenvectors from the canonical analysis of *γ* in Table 7 for mating success (sociosexual behaviour at T1).

	M		**Selection**	
	Male comp.	Fem. choice	$\boldsymbol{\Theta_i}$	$\boldsymbol{\lambda_i}$
Mating success				
$\boldsymbol{m_1}$	-.79	-.62	**-.15***	.08
$\boldsymbol{m_2}$	.62	-.79	.11	-.06

Note: The linear (*Θi*) and quadratic (*λi*) gradients of selection along each eigenvector are given in the last two columns. The quadratic selection gradients (*λi*) of each eigenvector (m_i) are equivalent to the eigenvalue. Male comp. = male-male competition; fem. choice = female choice; randomization tests: **p*<.05.

Selection analyses when using subjective ratings as predictors. Following Hill and colleagues (2013), we substituted the objectively measured sexually dimorphic traits by target men's observer-rated bodily, facial and vocal sexual attractiveness and physical dominance (see also models 2, 4, 6, 8, and 10 above), in order to capture subjective impressions, which may yield information beyond the specificity of the measured objective traits.

Facial, bodily and vocal attractiveness were under positive linear selection due to female mate choice (in terms of selection gradients for the former two, and selection on the eigenvector m_3 for the latter; Tables S7A and S8A). Facial and vocal attractiveness were positively, and bodily attractiveness was negatively, linearly associated with success under male-male competition (selection gradients and/or related eigenvectors; Tables S7B and S8B). However, none of these observer-rated attractiveness variables or related eigenvectors showed associations with mating success (Tables S7C and S8C). One significant eigenvector each revealed a positive (m_3) and a negative effect (m_5) of bodily dominance on female mate choice (Table S8A). Facial, bodily and vocal dominance were positively linearly related to male-male competition (in terms of selection gradients and/or an eigenvector m_2, m_3 and m_5; Tables S7B and S8B), of which only bodily and facial dominance were positively linearly related to mating success (selection gradients and the related eigenvector m_4, respectively; Tables S7C and S7C). No nonlinear selection was detected under female choice, male-male competition or mating success (Tables S7A/B/C and S8A/B/C). As with objective traits, the strength and form of linear sexual selection acting on the six male traits differed significantly between female choice and male-male competition ($F_{6,272}$=5.08, p<.001; Table S9). This was due to selection for greater facial attractiveness ($F_{1,272}$ = 7.36, p < .01), bodily dominance ($F_{1,272}$ = 6.20, p =.01) and bodily attractiveness ($F_{1,272}$ = 4.08, p =.04) through male-male competition. There was no difference in quadratic ($F_{6,260}$=0.18, p=.98) or correlational sexual selection ($F_{15,230}$=0.62, p=.86; Table S9).

Discussion

Employing a partly longitudinal design and an extensive set of both objectively measured and observer-rated putative sexually dimorphic traits, we provide evidence for a stronger role of male-male competition than female mate choice in sexual selection on German men. Our main findings are that physical dominance rated by men based on videos (as a proxy measure of male-male competition), but not female-judged sexual attractiveness (as a measure of female mate choice), predicts men's mating success, measured as their sociosexual behaviour (Penke & Asendorpf, 2008). This association held both cross-sectionally (T1) and quasi-longitudinally (T2, 18 months after T1) and was shown using structural equation modelling (SEM), as well as multivariate selection analysis and canonical analyses (for T1 only). Using the number of sexual partners in the previous twelve months as an alternative indicator of mating success (as in Hill et al., 2013) with no overlap between T1 and T2, this association could be replicated only cross-sectionally, but not longitudinally. Neither male-male competition nor female choice longitudinally predicted an alternative measure of men's mating success, the number of potential conceptions (NPCs; Perusse, 1993). The sociosexual behaviour measures overlapped at T1 and T2, since two out of the three items asked for the lifetime number of partners. Consequently, these analyses are only quasi-longitudinally. In contrast, for the number of sexual partners within the previous twelve months and the NPC index there is no overlap, so that these are longitudinal results, providing insight into potential causation. Not surprisingly due to the strong correlation between sociosexual behaviour at T1 and T2, we could replicate the positive effect of physical dominance on sociosexual behaviour at both time points. However, this was not the case for the number of sexual partners, which might be a false negative, explicable by the considerably lower power at T2. In addition, the twelve months represent a rather short time frame, so that for most men there are only few occurrences of new sexual partners, reducing the variable's variance and decreasing the likelihood of finding an effect. For the NPC index we found no effects of male-male competition or female choice, for which there are several possible reasons. First, T2 sample size and thus power was also low for analyses involving NPCs. Also, four participants did not fully complete this measure but did indicate comparatively large numbers of sexual partners by T2. Thus their NPCs values could not be calculated, but would presumably have been towards the upper end of the distribution, so that this measure is somewhat biased. It should also be noted that the NPC index has not been used very often in empirical studies since its publication 25 years ago, so that it cannot be seen as well validated. Alternatively, assuming the index and our findings are valid, it may mean that male-male competition predicts male number of sexual partners, but is unrelated to the frequency of sexual intercourse with them. This argument may be related to the diminishing returns in terms of conception for repeated copulations with the same woman (Kanazawa, 2003). Our findings could imply that men's traits related to mating competition function primarily to increase the number of mates, but not copulation frequency. Despite our null results, the NPCs may be a promising candidate for future studies on human sexual selection, capturing mating success more thoroughly.

Regarding the objectively measured sexually dimorphic traits, both kinds of statistical analyses consistently indicated a positive linear effect of men's physical strength, and a negative curvilinear effect of upper body size on female mate choice, suggesting stabilizing selection. Some inconclusive significant effects on female mate choice were shown for body height (positive linear), vocal fundamental frequency and upper body size (negative linear for both), which need to be replicated in further research. These results for upper body size and body height are partly in line with Hill and colleagues (2013), who found a curvilinear effect of girth and a positive linear effect of body height.

Moreover, Puts and colleagues (2016) reported a small negative linear effect of fundamental frequency on perceived dominance, which we replicated here. Both kinds of analyses converged on positive associations of upper body size and physical strength, as well as positive curvilinear (disruptive) and negative curvilinear associations of body height and upper body size, respectively, with male-male competition. The positive linear association for upper body size aligns with Hill and colleagues' finding for their aggregate measure girth. Inconsistent findings for selection under male-male competition were detected for fundamental frequency and body height (negative linear), baseline testosterone (T, both negative and positive linear loadings on eigenvectors), and physical strength (negative curvilinear), as well as negative correlational selection between body height and physical strength and positive correlational selection between fundamental frequency and physical strength. Although these results partly support previous findings (at least for fundamental frequency: Hill et al., Puts et al., Saxton, Mackey, McCarty, & Neave., 2016), they need to be replicated in future research. Consistent positive linear effects on mating success (sociosexual behaviour at T1) were found for male-male competition and upper body size, both supporting findings by Hill and colleagues. Partly significant positive linear effects on mating success were shown for female mate choice, body height, and baseline T, providing some support for Hill and colleagues' positive linear effect of body height. Finally and importantly, canonical analyses suggested the association of mating success (sociosexual behaviour at T1) with male-male competition was significantly stronger than with female mate choice (replicating Hill and colleagues' finding).

Thus, we could only partly replicate results regarding fundamental frequency (Puts et al., 2016; Saxton et al., 2016), which has been described as one of the most highly sexually dimorphic traits in humans (Puts, Doll, & Hill, 2014). Our lack of detecting a significant effect of body height on mating success converges with previous studies showing a mixture of positive and negative, linear and quadratic associations between height and reproductive success (e.g., Nettle, 2002; Stulp, Pollet, Verhulst, & Buunk, 2012). On the contrary, negative linear selection of height under male-male competition (at least in the canonical analyses) contradicts some previous findings indicating that taller men on average are more aggressive, physically stronger and are perceived to have better fighting ability (for a review see Stulp & Barrett, 2016). This result may be explained as an oddity of our sample. Our sample of target men seems to be characterized by a slight overrepresentation of short men who are muscular and hence appear dominant, and tall but slim men who were rated as low in physical dominance. Thus, this study's finding regarding the link between height and male-male competition should be treated cautiously and clarified in further studies.

We provide novel evidence for a likely influence of physical strength in men's sexual selection. In contrast, baseline T does not appear to be selected for under either female mate choice, male-male competition or mating success. Even though baseline T levels are highly sexually dimorphic (e.g., Cohen's *d*=3.20; Edelstein, Chopik, & Kean, 2011), and T has been suggested to be an underlying mechanism for trade-offs between mating and parenting effort in males (e.g., Muehlenbein & Bribiescas, 2005; Muller, 2017), and hence meets important criteria to be considered a sexually selected variable, we do not provide additional evidence for associations with men's perceived attractiveness (cf. Roney, Hanson, Durante, & Maestripieri, 2006), dominance (cf. Dabbs, 1997), or mating success (cf. Peters, Simmons, & Rhodes 2008; Puts et al., 2015). Thus, there may be no direct and unambiguous positive association between T levels and mating success, and further psychological variables may mediate or moderate the link. Alternatively, effects of T or any other sexually dimorphic trait mediating men's reproductive success (Puts, 2016) may not satisfactorily be captured by a simple measure of men's number of sexual partners. Instead, more qualitative assessment of men's reproductive effort, or a more complete investigation of their reproductive success, may deliver insights into the exact role of T levels and other traits in sexual selection. Furthermore, rather than current baseline T levels, pubertal and/or perinatal T levels may be more relevant in this context (e.g., Whitehouse et al., 2015), due to developmental links with traits implicated in sexual selection (Hill, Bailey, & Puts, 2017), such as physical strength (Lassek & Gaulin, 2009). Alternatively, acute fluctuations in T have been suggested to be more strongly related to behaviours and traits than baseline T (Carre & Olmstead, 2015).

Some of our traits showed nonlinear selection, such as upper body size and body height, suggesting differential optimum levels (Saxton, Mackey, McCarty, & Neave, 2016). Our results indicate that women seem to favour men with medium levels of upper body size over very large and very small men, with a similar trend under male-male competition. In contrast, for body height, we found the opposite: in this study it appeared both small and tall, but not medium-sized men are selected for under male-male competition. The latter, however, may also be interpreted as a false positive finding, especially taking into account this sample's apparent oddity regarding body height (see above).

The physical dominance and sexual attractiveness of bodily, facial and vocal stimuli was also judged by unacquainted raters in order to capture subjective impressions of men's traits, complementing our objective measurements. We found robust positive linear selection for facial attractiveness under both female choice and male-male competition (supporting Hill et al., 2013 for female choice, but contradicting their result for male-male competition), as well as selection for increased facial and bodily dominance under male-male competition, but not consistently under female mate choice. These findings are somewhat in line with previous suggestions that men's facial masculinity may not be preferred by women, since it conveys impressions of aggressiveness and may hence be more functional in male contests (Puts et al., 2012; Scott et al., 2014). Neither facial dominance nor attractiveness predicted mating success, partly contradicting previous findings (e.g., Mueller & Mazur, 1997). Regarding observer perceptions of vocal stimuli, we detected only an inconsistent effect of vocal dominance on male-male competition, partly backing previous findings on objective measures of vocal characteristics (e.g., Hill et al., 2013; Puts et al., 2016; Saxton, Mackey, McCarty, & Neave, 2016). Overall, facial attractiveness robustly predicted female choice, and bodily dominance, facial dominance and attractiveness were related to male-male competition, which predicted mating success. These somewhat mixed findings regarding the role of men's facial dominance and attractiveness in sexual selection require further investigation.

Mediation analyses revealed that male-male competition mediated the association of men's sociosexual behaviour with objectively measured upper body size and physical strength, and observer-judged vocal dominance, facial dominance and attractiveness. Female mate choice did not have mediating effects. The mediation effects concerning upper body size and physical strength nicely show how men’s formidability may lead to success in male-male competition and subsequently higher mating success. This reveals how these two putative sexually selected traits may have been and are currently under positive linear selection, by augmenting men’s access to mates and thereby increasing reproductive success. These findings converge with two more ecologically valid results from two studies in small scale societies. In one Western African population, men involved in traditional ritual fights (wrestling) had a higher number of offspring, but were not especially preferred by local women (Llaurens, Raymond, & Faurie, 2009). In another traditional society, men’s success in turtle hunting predicted earlier onset of reproduction and higher reproductive success, but again this activity did not appear to be valued by women (Smith, Bliege Bird, & Bird, 2003). Thus, traits related to physical dominance may enhance men’s access to opposite-sex mates and increase their mating and reproductive success, supporting a strong influence of male-male competition and related traits in men’s sexual selection.

Our study offers several improvements over previous studies. Besides including men’s sexually dimorphic traits examined in earlier studies (e.g., fundamental frequency, body height, upper body size; Hill et al., 2013; Puts et al., 2016), we included additional relevant traits, such as physical strength and baseline T. We extended Hill and colleagues’ approach of assessing subjective impressions of men’s vocal and facial traits by asking male and female raters to judge men’s bodily dominance and attractiveness from valid 3D body stimuli, which likely capture more information than simple objective measures, thus strengthening the validity of findings on sexual selection mechanisms (Doll, Cardenas, Burriss, & Puts, 2016). We employed additional mating success measures to more thoroughly characterize men’s mating success. Besides using sociosexual behaviour (SOI-R; Penke & Asendorpf, 2008), we conducted our analyses with the number of sexual partners in the previous twelve months, in order to directly replicate findings by Hill and colleagues. Additionally, we assessed NPCs (Perusse, 1993), an index that takes into account the number of copulations with each partner.

Our indices of mating success, despite possibly being broader than in previous studies, should still be considered indirect proxies of reproductive success. It may well be that some men have a large number of sexual partners during their young adulthood, but may not convert this quantitative mating success into a high reproductive success later in life. Although NPCs (Perusse, 1993) may be a more valid proxy of mating success than a simple count of sexual partners, it is still far from measuring actual reproductive success, and closer to fertility than to reproductive success (Steven, 1993). Still, previous evidence suggests that measures of mating success may be moderately related to men's reproductive success (Puts, Bailey, & Reno, 2015). Relatedly, our mating success measures were self-reports, which have been shown to be biased in some cases, especially for men (e.g., Smith, 1992). Such a bias may be moderated by personality, in that more dominant men may exaggerate their self-reported number of sexual partners even more, consequently inflating the association between rated physical dominance and sociosexual behaviour.

In addition to objective measures, men's sexually dimorphic traits were assessed via subjective ratings. Whereas our objective measures assessed a single or a few cues of men's traits (e.g., vocal fundamental frequency, handgrip and upper body strength, baseline T), our subjective ratings focussed on a more integrated assessment of different aspects based on separate entities of a man's phenotype. For example, raters judging vocal dominance and attractiveness (unconsciously) base their assessment on traits' perceptual components beyond fundamental frequency, such as formants or harmonics. Hence, these subjective ratings provide a more complete assessment of men's phenotype with a focus on two crucial emergent characteristics (dominance and attractiveness) of three aspects (faces, bodies, voices). The validity of attractiveness and dominance ratings based on facial photographs and vocal stimuli has been supported in previous studies (e.g., Doll et al., 2014). Relatedly, the video-based judgments of physical dominance and sexual attractiveness, as proxy measures of the two primary mechanisms of sexual selection, were based on an even larger number of cues, since raters observed an individual's behavioural sequence, including visual and verbal information. Thus, these judgments are more complete and valid assessments of a target man's physical dominance and sexual attractiveness, which justifies their positioning as a potential mediator of the association between objective traits or subjective ratings and mating success. Still, reports from well-acquainted peers, as used in Hill and colleagues' study (2013), are likely even more valid ways of capturing real-life physical dominance and sexual attractiveness.

In this study we focused on men's sexually dimorphic, objectively measured traits, which have partly been investigated in previous research, as well as subjectively judged impressions of attractiveness and dominance, based on stimuli which were assumed to be the most important in mate choice and intrasexual competitions (voices, faces and bodies). Besides these traits and observer impressions, men's self-reported psychological traits could be assessed in relation to their mating and reproductive success and a potential influence of perceptions of physical dominance and sexual attractiveness. For example, propensity for same-sex aggression, pain tolerance, risk-taking, interest in physical competition and coalition formation (Puts, Bailey, & Reno, 2015) could be investigated, which presumably are more strongly implicated in male-male competition, but may also affect perceptions of attractiveness. Vall and colleagues (2016) found seven dimensions of personality pathology to be under sexual selection in men and women. For example, persistence-compulsivity was shown to have positive effects on men's reproductive success (mediated by relationship duration, fatherhood and number of offspring). Thus, future studies could focus on the role of relevant personality traits in sexual selection.

To further disentangle the relative contributions of male-male competition versus female choice to sexual selection in men generally, further research could investigate females' perceptions of men's physical dominance, to pinpoint if it is actually more physical dominance amongst men which leads to increased access to potential female partners (as in our study), or whether females prefer and choose more dominant men directly. This would also yield additional insights into female mate choice, enabling us to examine whether female-rated physical dominance predicts men's mating success, and more so than female-rated sexual attractiveness. On the other hand, though it has been suggested that sexual selection may have affected men more than women (Puts, 2010, 2016), intrasexual competition and male mate choice likely also influenced the evolution of women's phenotypic traits (Arnocky & Vaillancourt, 2017; Fink, Klappauf, Brewer, & Shackelford, 2014). To our knowledge, there is no comprehensive study on women comparable to the current study or Hill and colleagues (2013). Presumably, male mate choice would be more influential here, but female competition should not be underestimated (Arnocky, 2016).

An important question concerns whether there are cross-cultural differences in the relative contributions of different mechanisms and sexually dimorphic traits to sexual selection, especially given that societies differ in potentially influential moderating variables such as mating systems and subsistence types (Hill et al., 2013; Schmitt, 2015). This study could be replicated in more traditional and collectivistic societies (in contrast to the highly industrialized and individualistic German population) to further explore the complex evolutionary dynamics underpinning sexual selection.

Finally, a study on sexual selection remains incomplete until the full array of possible mechanisms has been investigated. Besides mate choice and direct intrasexual competition, these include scrambles, sexual coercion, and sperm competition (Puts, 2016). Though the latter three mechanisms may have played some role over human evolution and are prominent in nonhuman animals (Puts, 2010), direct intrasexual competition and mate choice are arguably the primary mechanisms in human sexual selection. Our study adds further evidence that of these, direct intrasexual competition may be more influential. Still, future research could investigate to what extent scrambles, sexual coercion and sperm competition are related to men's sexually dimorphic traits and affect mating and reproductive success (Barbaro & Shackelford, 2016; Goetz & Shackelford, 2006; Leivers, Rhodes, & Simmons, 2014). Our findings of men's formidable traits affecting success in male-male competition, which subsequently predicted mating success, point towards male intrasexual competition remaining still playing a role in this contemporary industrialized Western population. The intensity of men's contest competition throughout human evolution may be underestimated when examining traits such as upper body size and physical strength, due to the invention of tools enabling to aggress from a distance, such as handheld weapons, limiting the usefulness of anatomical weaponry

(Hill, Bailey, & Puts, 2017). With modern laws and societal norms suppressing overt aggressiveness, such formidable traits may no longer function in direct male contests. Instead, these traits may lead to elevated prestige and respect in dyadic relationships and groups, which may subsequently enhance a man’s access to potential female partners. This is supported by earlier findings that men’s social dominance and status are related to mating and reproductive success (Puts, 2016; Vall et al. 2016; von Rueden & Jaeggi, 2016; see Arnocky & Carré, 2016, for a discussion of different kinds of male-male competition). For example, a study by von Rueden, Gurven and Kaplan (2011) examined the relative influence of both physical and social dominance on men’s reproductive success in the Tsimane. They showed that whereas both predicted a higher reproductive success, the effect of social dominance was somewhat stronger. Further sexual selection studies could investigate variables such as prestige, popularity or social status as potential mediators between success in male-male competition and mating/reproductive success, as these may explain such relationships in contemporary societies characterized by reduced overt aggressiveness (Puts, Bailey, & Reno, 2015; see von Rueden & Jaeggi, 2016, for a comprehensive meta-analysis in nonindustrialized societies). Moreover, rather than physical prowess, traits like intelligence and humor may influence status, dominance and subsequently mating success, and may hence be under sexual selection in modern societies (Miller, 2000; Prokosch, Coss, Scheib, & Blozis, 2009). Still, considering the complexity of contemporary social interactions generally and mate choice specifically, our finding of positive effects of male-male competition and (inconsistently) female choice on sociosexual behaviour also point towards the likelihood of intrasexual competition and female choice acting in concert, for instance that women find dominant men attractive, or seek their protection and provisioning abilities, and subsequently choose them as their partners (Puts, Bailey, & Reno, 2015). Our lack of finding an interaction between male-male competition and female choice on mating success shows that their effects may well be additive, questioning previous claims of correlational selection for these two mechanisms of sexual selection (Hunt, Breuker, Sadowski, & Moore, 2009). Additional work is required to disentangle the contributions of female mate choice and male-male competition to men’s sexual selection.

An important question surrounds the distinction between current selection and adaptation (i.e., past selection): Do we provide evidence for selection in progress or rather selection during humans' early evolution, which may not necessarily be ongoing (Puts, Bailey, & Reno, 2015)? It has been argued that trait-related approaches, as ours, are more useful to provide insights into adaptation rather than current selection (Grafen, 1987). Different types of evidence are required to conclude that a trait has been influenced by sexual selection in the past. Traits should develop or increase in expression around sexual maturity, and show sexual dimorphism (Hill, Bailey, & Puts, 2017). These preconditions are likely fulfilled for all five objectively measured traits in this study (fundamental frequency, baseline T, upper body size, body height, and physical strength; e.g., Mehta & Josephs, 2010; Price, Dung, Hopkins, & Kang, 2012; Puts, Doll, & Hill, 2014; Puts et al., 2016). Moreover, a trait should affect success in one or more mechanisms of sexual selection and eventually mating success. We provide further evidence for such effects at least for upper body size and physical strength. Thus, under these assumptions there appears to be strong indication of past sexual selection on increased upper body size and physical strength (Hill, Bailey, & Puts), replicating and extending previous research (e.g., Hill et al., 2013). However, on the contrary, since we assessed men's current mating success and hence a proxy for adaptiveness, we cannot be sure that these traits were adaptive throughout humans' environment of evolutionary adaptedness. This is complicated by the fact that developments in modern industrial environments such as contraception and normative monogamy may confound associations between dominance- and attractiveness-related traits and reproductive success, and even mating success (Perusse, 1993). Therefore, our approach is more a behavioural ecological one, though we still assume that our findings provide insight into past sexual selection on men's traits (Hill et al., 2013; Hill, Bailey, & Puts, 2017).

Overall, we provide evidence for a stronger influence of male-male competition, compared to female mate choice in sexual selection on men. Men with higher physical dominance, but not sexual attractiveness, indicated higher mating success. Moreover, male-male competition mediated effects of upper body size, physical strength, facial attractiveness, as well as vocal and facial dominance on mating success. We hence deliver novel insights for an important role of physical strength, but not for baseline testosterone, in sexual selection on men. Thus, access to female mates may be predominantly determined by intimidating, competing with and winning against male rivals, rather than by being perceived as attractive and chosen by females.

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5. General Discussion

Summary of the main findings

In this dissertation, different facets of men's competitive behaviour were investigated, including personality psychological, endocrinological, life history and sexual selection perspectives. In Manuscript 1 we detected an acute reactivity of the androgenic steroid hormone Testosterone (T) in men engaging in a dyadic intrasexual competition, while being exposed to an attractive female confederate (experimental group, relative to a control group). Moreover, we found personality state and social impression changes in facets like competitiveness, dominance and self-assurance, as well as associations of these personality state changes with T reactivity (partly attenuated by high baseline Cortisol (C) levels; Table 1). Personality state changes were not only reported by the male participants themselves, but also reliably perceived by unacquainted observers. In Manuscript 2, we examined the role of men's sexually dimorphic traits in male-male competition, female mate choice and consequently sexual selection. In a partly longitudinal design, a stronger influence of male-male competition and related traits such as physical strength and upper body size, compared to female choice, on men's mating success was revealed (at least for two of the three mating success measures; Tables 2 and 3).

Table 1

Overview of results for preregistered hypotheses for the first Manuscript's Studies 1, 2b and 3b

	Self-reports	Observer-ratings	
Hypotheses	IAL (Study 1)	IAL (2b)	Social impressions (3b)
1) T reactivity[a]	1st, not 2nd T *post*-sample	-	-
2) personality state changes[a]	competitiveness (BC), coldheartedness (DE)[c], ingenuousness (JK)[c]	dominance (PA), competitiveness (BC), submissiveness (HI), ingenuousness (JK)	self-display, self-assurance
Not supported for:	dominance (PA), extraversion (NO), nurturance (LM), introversion (FG)	-	cooperativeness
3) personality state changes & T reactivity[b]	competitiveness (BC; 1st, not 2nd T *post*-sample)	dominance (PA; 2nd, not 1st T *post*-sample)	self-assurance (1st, not 2nd T *post*-sample)
Not supported for:	dominance (PA), extraversion (NO), nurturance (LM), introversion (FG)	competitiveness (BC), submissiveness (HI), ingenuousness (JK)	cooperativeness, self-display
4) personality state changes & TxC[b]	competitiveness (BC; 1st & 2nd T *post*-sample), dominance (PA; 1st T sample only)	-	-
Not supported for:	dominance (PA), extraversion (NO), nurturance (LM), introversion (FG)	dominance (PA), competitiveness (BC), submissiveness (HI), ingenuousness (JK)	cooperativeness, self-display, self-assurance

Note. T = testosterone; TxC = T reactivity x baseline cortisol interaction; IAL = interpersonal adjective list (see Figure 1); [a] relative changes, experimental versus control group (N = 164-165); [b] experimental group only (n = 124); [c] hypothesis not preregistered; results of Studies 2a and 3a largely overlapped with 2b and 3b, respectively (see Manuscript 1 for details).

Table 2

Overview of results for the second Manuscript's findings, consistent across both kinds of analyses

IV (selected for)	DV (selection under)	Significant effects
Objective traits[a]	Male-male competition	(+) physical strength, (+)/(c-) upper body size, (c+) height
Objective traits[a]	Female choice	(+) physical strength, (c-) upper body size
Objective traits[a]	Mating success	(+) male-male competition
Subjective ratings[b]	Male-male competition	(+) facial attractiveness, (+) facial dominance), (+) bodily dominance
Subjective ratings[b]	Female choice	(+) facial attractiveness
Subjective ratings[b]	Mating success	-
Competition/mate choice	Mating success	(+) male-male competition

Note. IV = independent variable; DV = dependent variable; [a] objective traits: physical strength, upper body size, height, fundamental frequency, baseline testosterone; [b] subjective ratings: facial, bodily and vocal attractiveness/dominance; (+)/(-) significant positive/negative linear effect; (c+)/(c-) significant positive/negative curvilinear effect; mating success measured as sociosexual behaviour at time point 1 (*N* = 164; for the other mating success measures, see Table 3 and Manuscript 2); two analyses: structural equation models and selection/canonical analyses (curvilinear effects and associations between traits/ratings and mating success for the latter only).

Table 3

Effects of male-male competition and female mate choice on mating success at time points 1 and 2 in Manuscript 2

Mating success measure	T1	T2
Sociosexual behaviour	Male-male competition	Male-male competition
Sexual partners 12 months	Male-male competition	-
Number of potential conceptions	-	-

Note: Sexual partners 12 months = number of sexual partners within the previous 12 months; T1/T2 = time point 1/2 (*N* = 164/109).

Theoretical implications

The results of our studies showed not only acute hormonal and personality state changes acting in concert, but also that related traits, such as dominance, physical strength and upper body size, are implicated in sexual selection and appear to function in acquiring female mates. The studies in Manuscript 1 extend findings from previous research on the role of hormonal fluctuations in competitive situations. The T increase, which was partly larger in the experimental group following a competitive interaction than in a control group, supports predictions derived from the challenge hypothesis (Archer, 2006; Wingfield, Hegner, Dufty Jr, & Ball, 1990), replicating previous studies showing T responses in men after interacting with a potential female partner (e.g., Roney, Lukaszewski, & Simmons, 2007) and after engaging in intrasexual competition (e.g., van der Meij, Buunk, Almela, & Salvador, 2010). T reactivity also appeared to be linked with personality state changes in domains relevant to this intrasexually competitive context (Table 1). As these personality facets relate to aspects of social status (Eisenegger, Haushofer, & Fehr, 2011; Mattan, Kubota, & Cloutier, 2017), our findings converge with predictions from the biosocial model of status (Mazur 1985; Mazur, Welker, & Peng, 2015), according to which fluctuations in status should be linked with T levels.

Our findings fit well into previous claims that acute T fluctuations may be functional in modulating a trade-off between, on the one hand, competition and mating, and, on the other hand, nurturing and parenting behaviours (Muehlenbein & Bribiescas, 2005; Muller, 2017; Roney, 2016; Zilioli & Bird, 2017). These trade-offs imply unidimensional associations between T and behaviours, with low and high T levels related to nurturing/parenting and competition/mating, respectively. Earlier studies have reported associations between T and personality (albeit on a trait level; Turan, Guo, Boggiano, & Bedgood, 2014), using the same personality model as in our study, the interpersonal circumplex (Wiggins, 1982; see also Figure 1). Because the interpersonal circumplex’ two main axes (i.e., Dominance and Love, largely corresponding to the dimensions of competition/mating and nurturing/parenting) are defined as being orthogonal to each other, rather than unidimensional, the question arises how T and personality are associated on a state level. Our findings of positive associations of T reactivity with changes in self-reported competitiveness and observer-perceived dominance can be interpreted as suggesting a unidimensional relationship, in that no association with any of the orthogonal axes (such as nurturance-coldheartedness or extraversion-introversion; Figure 1) emerged. Moreover, we did not detect correlations between baseline T levels and personality traits, failing to replicate findings of Turan and colleagues (2014) and Sellers and colleagues (2007). Thus, it seems T and personality are more reliably related on a state, intra-individual level (e.g., Carré & Olmstead, 2015), and more in a unidimensional than a bidimensional way. However, it needs to be acknowledged that our studies in Manuscript 1 were situated in a competitive mating context, so that a complete picture of T-modulated trade-offs and the comparison of uni- versus bidimensional relationships demands studying the other side, namely nurturing and partnering behaviours (for studies and reviews on these in relation to hormonal variables, see Gettler, McDade, Agustin, Feranil, Kuzawa, 2013; Gray, Campbell, Marlowe, Lipson, & Ellison, 2004; Gray et al., 2017; van Anders, 2013; Weisman, Zagoory-Sharon, & Feldman, 2014). Until our design of studying personality state changes in relation to acute T fluctuations is repeated in nurturing/partnering contexts, no final conclusions can be drawn on these relationships.

Further, the associations between self-reported personality state changes and T reactivity were partly attenuated by high baseline C levels (Table 1), in line with the dual-hormone hypothesis (e.g., Mehta & Josephs, 2010). This points towards an interaction between two endocrinological axes, the hypothalamus pituitary gonadal (HPG) and hypothalamus pituitary adrenal (HPA) axes, with the latter's end-product C buffering effects of the former's end-product T. These moderating effects were only detected for self-reported, but not observer-rated personality state and social impression changes.

Manuscript 1 contributes to the ongoing debate on the exact effects of T in human social interactions. It adds to previous studies showing that acute T fluctuations are related to competitive behaviour (e.g., Eisenegger, Kumsta, Naef, Gromoll, & Heinrichs, 2017) as one facet of status-seeking (e.g., Eisenegger, Haushofer, & Fehr, 2011). Moreover, we show that such T reactivity is associated with personality state changes in dimensions such as dominance and self-assurance, which are also perceptible by unacquainted observers. Our results stress the importance of considering T reactivity during social interactions as a key modulator of personality state changes and social behaviour (Carré, Baird-Rowe, & Hariri, 2014) and specifically suggest a potential role of hormonal reactivity in competition-related social signalling, whether intra- (to male rivals) or intersexually (to potential female mates). These findings imply hormonal reactivity and associated personality state changes as a proximate mechanism which may have evolved in order to support competitive and mate acquisition behaviour, in the pursuit of maximizing evolutionary fitness (Del Giudice, Gangestad, & Kaplan, 2015; Zilioli & Bird, 2017).

Manuscript 2 replicates and expands earlier studies, which already hinted towards a stronger role of male-male competition, relative to female mate choice, in sexual selection on men. Puts and colleagues (2016) focussed on vocal fundamental frequency, showing that associations with male-rated dominance were stronger than female-rated attractiveness. Hill and colleagues (2013) examined a selection of men's sexually dimorphic traits, both objectively measured and subjectively assessed, in relation to proxy indicators of male-male competition and sexual attractiveness as well as mating success. Their findings are largely in line with ours; the male-male competition measure and associated traits (girth and vocal masculinity), but not female mate choice, positively predicted mating success. Two studies (Llaurens, Raymond, & Faurie, 2009; Smith, Bliege Bird, & Bird, 2003) provided more ecologically valid results from traditional rural societies. Men involved in ritual fights (wrestling; Llaurens et al., 2009) and turtle hunting (Smith et al., 2003) were reproductively more successful (larger number of offspring, younger onset of reproduction and/or higher reproductive success), but were not especially preferred by local women. This further points towards a stronger impact of men's competitive behaviour, compared to their attractiveness to women, on components of evolutionary fitness. Hence, in Manuscript 2 we support these findings, showing their robustness in a relatively large sample, partly longitudinal design and across two kinds of statistical analyses. We provided evidence that at least in the Western population studied, male-male competition is still prevalent and influential in terms of men's mating success. It appeared that men still acquire (sexual) mates by intimidating and earning respect from other males, rather than by being perceived as attractive and chosen by women more directly. These mechanisms could partly be attributed to men's, compared to women's, larger reproductive variance, and the operational sex ratio (ratio of sexually active men to fecund women) being biased towards more men, intensifying male intrasexual competition (Hill, Bailey, & Puts, 2017).

Miller (2000) proposed four central questions research on sexual selection should focus on: how do traits differ between individuals, how can those differences be perceived during mate choice, how are those differences inherited, and how are they related to overall fitness? Manuscript 2 contributes further evidence to three of the four questions suggested by Miller: Inter-individual differences in men's sexually dimorphic traits, how these are perceived by unacquainted observers, as well as effects on mating success as a proxy of evolutionary fitness were assessed. Overall, these findings imply intrasexual competition is a major mechanism of sexual selection in men, which in turn is a type of natural selection (Andersson, 1994). Since sexual selection informs us about the evolution of sexually dimorphic traits, we can conclude from our study that primarily the mechanism of male-male competition had an influence on the development of men's formidable traits, such as physical strength and upper body size.

Both Manuscripts' findings can be interpreted as indicating life history trade-offs of allocating energy and resources to relevant tasks, such as intrasexual competition and mate acquisition (Del Giudice, Gangestad, & Kaplan, 2015). Zilioli and Bird (2017) suggested three evolutionarily relevant social contexts, in which such trade-offs should be especially implicated: competitive interactions, exposure to potential mates, and interactions with offspring. The studies of both Manuscripts focussed on the former two, whereby Manuscript 1 dealt with men's reactive behaviour in a concrete competitive mating situation, and in Manuscript 2 proxy measures of men's success in these situations were analysed (physical dominance and sexual attractiveness). Manuscript 1 added evidence for a T-modulation of these trade-offs, and showed associations with personality state changes, which are potentially functional in social signalling and hence intrasexual competition and/or mate acquisition.

In turn, Manuscript 2 showed that the development of men's sexually dimorphic traits may have been influenced more by male-male competition than female mate choice, constituting a more ontogenetic trade-off in the pursuit of maximizing evolutionary fitness (Del Giudice, Gangestad, & Kaplan, 2015). Accordingly, while studies in both Manuscripts provide evidence on proximate mechanisms, the findings of Manuscript 1 have some phylogenetic relevance, because steroid hormones and their reactivity seem to be highly conserved across species (Carré & Moreau, 2015; Zilioli & Bird, 2017). Moreover, Manuscript 2 informs about potential ontogenetic and functional mechanisms by measuring the influence of sexual selection on sexually dimorphic traits and their effects on a proxy of reproductive success, respectively. Consequently, this dissertation contributes evidence from different evolutionary perspectives regarding men's competitive behaviour (Tinbergen, 1963).

Findings in Manuscript 1 could also be interpreted in terms of person-environment fit, the match between individual and environmental characteristics, including potential consequences like an individual's satisfaction, commitment and engagement (Kristof-Brown & Guay, 2011). Applied to the intrasexually competitive situation, participants with a dominant, competitive and extraverted personality profile presumably would be especially motivated and attracted by the competition itself, the monetary incentives, and the opportunity to impress the attractive female confederate. Accordingly, moderating influences of personality traits on associations between personality state changes and T reactivity were examined in additional regression analyses, and two significant effects were found. First, there was a moderation of the association between ingenuous state changes and T reactivity by trait-competitiveness; participants increased more in ingenuousness with higher T reactivity when trait-competitiveness was low (for the second *post*-sample only; β = -1.15, p = .01). This could be interpreted as men low in competitiveness further shying away from competition (increase in ingenuousness) with larger T increases. Secondly, there was a positive association between an increase in a nurturing state and T reactivity in men low in ingenuousness (i.e., high in competitiveness; for the first *post*-sample only; β = -1.23, p = .045; all others, for both *post*-samples: unsigned βs < 1.15, ps > .052). This could mean that at least some competitive men (low in ingenuousness) try to gain status in a warm and nurturing way, when experiencing an acute T reactivity. This in turn can be seen as in line with earlier suggestions that T may not only modulate status-seeking in a dominant and aggressive, but also in a cooperative and communal way (see, for example, Eisenegger, Haushofer, & Fehr, 2011; Eisenegger, Naef, Snozzi, Heinrichs, & Fehr, 2010; van Honk, Montoya, Bos, van Vugt, & Terburg, 2012). Of course, further research is required to see whether these results are robust and meaningful. Additionally, bivariate correlations between personality traits and T reactivity were examined, to tackle the question whether people who are high in certain relevant traits, such as dominance, competitiveness or extraversion, would react more to the competitive mating situation in terms of hormonal increases. No significant effects were detected (for all personality facets and both *post*-samples, unsigned *r*s < .15, *p*s > .10; experimental group only; Table S1). Thus, person-environment fit seems to have played at least a minor role in the first Manuscript's studies, in that men's personality traits were partly associated with their response to competitive and challenging aspects of the situation, at least in terms of effects on T reactivity and personality state changes.

Strengths and limitations

The studies in Manuscript 1 were distinguished by several features, such as measuring naturally induced T reactivity, studying two hormones acting in concert (the importance of which has been stressed by Roney, 2016), as well as recording men's "slices of behaviour" both in a calm (baseline) and in an aroused (reactive) state to investigate self-reported and observer-perceived personality state changes. A particular strength of these studies was that they were preregistered before data collection, decreasing questionable research practices (for instance, *p*-hacking or hypothesizing after results are known, harking; Munafo et al., 2017). However, because these partly exploratory studies constituted a novel approach, analysing hormonal reactivity and personality state changes in conjunction, no clear hypotheses could be derived regarding for which specific personality facets we would expect effects. Accordingly, tentative hypotheses were preregistered for several facets which might be implicated in an intrasexually competitive context, of which some, but not all, hypotheses received support (see Table 3 in Manuscript 1). For these preregistered hypotheses, we used one-tailed significance tests halving the *p*-values (but most findings were still significant at $\alpha = .05$ without doing so). Furthermore, we assessed two *post*-saliva samples for T reactivity measures, as from previous studies and theorizing it was not clear when measures of T fluctuations would be most valid (for recommendations of a delay of 15-20 mins after a stimulation, see Casto & Edwards, 2016; Schultheiss, Schiepe, & Rawolle, 2012). We detected most significant effects only for the first *post*-sample (see Table 1). Thus, because we tested a large number of hypotheses twice (for two T reactivity measures), some findings might be false positives due to multiple testing and need to be treated cautiously. Still, our studies provide guidelines for more specific replications.

In contrast, the study in Manuscript 2 was not preregistered, mainly because we used data from the studies in Manuscript 1 and had not planned such a follow-up study when initially preregistering these. As hypotheses were derived from previous studies, especially Hill and colleagues (2013), the possibility of harking was limited. Another typical questionable research practice, continuing to collect data when results are not significant, was prevented by the simple fact that analyses were conducted on existing data. All participants were invited to the follow-up online questionnaire and responded voluntarily, only one participant was excluded from all analyses for indicating a bisexual orientation, which can be justified in this study on heterosexual men's mating success. In addition, most findings were robust across two different kinds of statistical analyses, including the simultaneous assessment of two central mechanisms of sexual selection and their interaction (total sexual selection; as recommended by Hunt, Breuker, Sadowski, & Moore, 2009), as well as both linear and curvilinear effects.

The sample sizes in Study 1 of Manuscript 1 ($n = 125$ in the experimental group) and in Manuscript 2 (T1/T2: $N = 164/109$) had sufficient power (80 %, given $\alpha = .05$, two-tailed test) to detect effect sizes of Pearson's $r > .24$ and $r > .21/.26$, respectively (Cohen, 1992). Because some of our hypotheses in Manuscript 1 were preregistered we decided to use one-tailed statistical tests for these (Cho & Abe, 2013; Lakens, 2016), which logically show superior power compared to two-tailed tests.

With a sample size of $n = 125$ they had sufficient power (> .80) for effect sizes of $r > .21$, thus being sensitive for detecting smaller effects than two-tailed tests. However, it has been argued that rather than 80 %, a power level of 90 % may be more desirable and produce more robust findings (e.g., Button et al., 2013; Maxwell, Lau, & Howard, 2015). Assuming such a higher level of power (for two-tailed tests) and sample sizes as indicated above ($n = 125$/ $N = 164$), effects greater than $r = .28$ and $r = .24$ would have been found in Manuscripts 1 and 2, respectively. Post-hoc power analyses (which, however, have been criticized earlier; see Hoenig & Heisey, 2001, for instance) yielded an observed power of 70.5% for the effect of T reactivity on self-reported competitiveness changes in Study 1 in Manuscript 1 (*partial* $\eta^2 = .04$; Cohen's $f^2 = .04$; one-tailed test; $n = 124$) and 93.6 % for the relationship between physical dominance and sociosexual behaviour at T1 in Manuscript 2 (linear regression, including sexual attractiveness as a covariate; *partial* $\eta^2 = .07$; Cohen's $f^2 = .08$; two-tailed test; $N = 157$), respectively. This indicates that statistical power was satisfactory to good for most analyses in both Manuscripts' studies (slightly better for T1 in Manuscript 2). Still, some real effects might have been missed as false negatives. Finally, our results were shown to hold when including several (partly preregistered) control variables as covariates, such as participants' age and relationship status. Overall, both Manuscripts' results can be seen as relatively robust, but further replication using even larger samples is called for, yielding greater statistical power, also to determine their generalizability to different samples and populations, and in more naturalistic settings (Figueredo et al., 2005).

Moreover, in Studies 2b and 3b (Manuscript 1) we conducted improved observer-ratings, compared to Studies 2a and 3a. In 2b an overall larger number of items per target man was divided into five item groups (and rated by 10 raters each; see Methods in Manuscript 1), yielding simultaneously increased reliability of personality state measures and reducing strain on the rater, and both negative and positive items were included in 3b for an increased reliability. Besides the experimental group, ratings were administered for the control group as well, in order to analyse differential *pre-post* changes in observer-perceptions to partial out practice effects. In these two improved replications, we could support most of the effects of Studies 2a and 3a (for details, see

Manuscript 1), providing robust findings. In Manuscript 2, we employed a partly longitudinal design (timespan: 18 months), in which we directly replicated the effect of male-male competition, but not female mate choice, at T1 on men's mating success at T2 (for sociosexual behaviour, but not for the number of sexual partners within the previous 12 months; no effect at T2 for the number of potential conceptions). Thus, both Manuscripts included follow-up studies in terms of direct and conceptual replications, to examine the findings' robustness and generalizability.

In both Manuscripts, a heterosexual mating system has been assumed, in that women are choosing men as their mates, and men compete with other men to impress and attract female potential partners. Future research could investigate how exactly mechanisms of hormonal reactivity and personality state changes, as well as sexual selection, function in homosexual relationships (for instance, Neave, Menaged, & Weightman, 1999 showed higher baseline T levels in homosexual, compared to heterosexual, men and women, respectively). Besides being restricted to a heterosexual mating system, both Manuscripts' studies had limitations in their design and results. In Manuscript 1, internal consistency for some self-reported personality state facets was moderate only, in particular for the facet competitiveness, for which we found an association with T reactivity (experimental/control group, *pre*: Cronbach's α = .69/.61, *post*: α = .60/.65; see Manuscript 1 for more details). This is likely due to item selection, as out of the originally eight items per facet (Jacobs & Scholl, 2005) we selected five, also for reasons of brevity. Internal consistencies for the observer-rated states were higher (α > .75 in Studies 2a and 2b; α > .77 in Studies 3a and 3b). This shows a reduced reliability of our self-reported personality states and calls for replication using the full facets. In Manuscript 2, a central weakness is that we only assessed proxy measures of reproductive success. Even though measures such as the number of sexual partners have been shown to moderately strongly correlate with reproductive success (Puts, Bailey, & Reno, 2015), there may still be large and meaningful differences. Men may attain a high mating success during their young adulthood (an age group we focussed on in our study), but may eventually not achieve a high reproductive success till the end of their reproductive life span. The number of potential conceptions (Perusse, 1993) may be a more valid proxy of mating success than a simple count of sexual partners by additionally incorporating coital frequency with each sexual partner, but it is still far from measuring actual reproductive success. Our lack of finding an effect of male-male competition on the number of potential conceptions may either indicate that there is no real effect (when using a more comprehensive mating success measure), that only one component (number of sexual partners), but not the other (coital frequency), is related to male-male competition, or that the result constitutes a false negative due to low sample size at T2. Thus, even though we assessed men's mating success more thoroughly compared to earlier studies (e.g., Hill et al., 2013; Peters, Simmons, & Rhodes, 2008), our results' validity is somewhat questionable in terms of the mating outcomes, warranting replication (ideally directly measuring reproductive success).

Future directions

A further study encompassing the conceptual replication and extension of both Manuscripts' studies would be to stage and observe an actual mating situation. Groups of single men and women would interact freely in an externally valid dating context, after their sexually dimorphic traits, baseline personality states and hormonal levels have been assessed. These interactions could be video recorded, in order to rate and code participants' mating and dominance behaviours by trained observers (as in van der Meij, Almela, Buunk, Fawcett, & Salvador, 2012). Afterwards, *post*-personality states and hormonal reactivity could be measured, and familiar female and male acquaintances could report on participants' physical dominance and sexual attractiveness. In a longitudinal design, similar to Manuscript 2, men's and women's mating or even reproductive success would be assessed, ideally in a longer time frame, to increase variance in their responses and hence reliability. Such a study would comprehensively investigate the conjunction of hormonal, personality and sexually dimorphic variables as well as mating outcomes in both men and women.

A crucial component of one's reproductive success and accordingly evolutionary fitness is, besides the number of sexual partners and one's own qualities, the partner's quality, the second parent of one’s offspring. Because extant studies typically assessed quantitative mating success, it would be relevant to measure qualitative mating success. Female partner quality entails aspects like fertility, and a typical indicator is, besides their age, physical attractiveness. A future study could set out to operationalize mating success as a combination of quantitative (number of sexual partners) and qualitative (partner physical attractiveness) characteristics, to yield a more complete proxy of evolutionary fitness in terms of reproductive success (see von Rueden & Jaeggi, 2016, for an extensive meta-analysis investigating the influence of different facets of men’s status on several measures of reproductive success, including ‘wife quality’). Ultimately, of course, the aim would be to measure men’s reproductive success at the end of their lifespan in a longitudinal design (with predictor variables measured during early adulthood, for example), and ideally also to assess offspring health and reproductive success.

The video-recorded self-presentations in Manuscript 1 yielded men’s "thin slices of behaviour" (Borkenau, Mauer, Riemann, Spinath, & Angleitner, 2004) firstly in a calm, baseline state and secondly in an aroused, reactive state (after a competitive situation). These were used to assess observer-perceptions as well as links with hormonal changes, in terms of interpersonal circumplex states and social impressions. Results of these global observer-perceptions indicated T reactivity may function in signalling to male rivals and potential female partners, by being related to increases in self-assurance and dominance. A study could set out to disentangle which facial and bodily features exactly convey such impressions, for example by more objectively coding gestures and mimics, focussing on emotions, speech duration and dominant versus submissive body postures (Mazur, 2005). This would inform us about which behaviours mediate changes in observer-perceptions, facilitating social signalling. The bodily, facial and vocal stimuli used in the study in Manuscript 2 could also be further investigated regarding objective characteristics (e.g., body measures, facial width-to-height ratio, facial asymmetry, and vocal fundamental frequency/formants), providing insights into which features partly explain observer-judgments of men’s physical dominance and sexual attractiveness. In addition, observer-perceptions of interpersonal circumplex states and social impressions in Manuscript 1 and of success in male-male competition and female mate choice were based on video recordings of individual men standing in a room alone and talking about their strengths; a direct competitive interaction between men and mating situation could be recorded instead (see van der Meij, Almela, Buunk, Fawcett, & Salvador, 2012, for a similar design). These may yield more externally valid observer-judgments regarding their social behaviour, which in turn could be analysed in conjunction with hormonal reactivity. Thus, even though we assessed observer-perceptions in a relatively comprehensive way (for example, employing both circumplex personality states and social impressions in Manuscript 1, and ratings based on four different kinds of relevant stimuli in Manuscript 2), men's dominant and mate attraction behaviours could still be assessed more objectively, and investigated in more ecologically valid ways in future studies.

The studies in Manuscript 1 predominantly focussed on proximate mechanisms and Manuscript 2 on functional outcomes, and some findings could be interpreted in terms of ontogenetic mechanisms (see above). Consequently, an evolutionarily account of men's competitive behaviour, requiring the analysis of all four perspectives (Tinbergen, 1963), is not yet complete. Future studies could further investigate ontogenetic effects (such as hormonal and personality state changes in a competitive context in childhood and adolescence, or adolescent traits as early predictors of mating/reproductive success). Findings of Manuscript 1 may already have some phylogenetic relevance, in that steroid hormones and their reactivity seem to be highly conserved across species (Carré & Moreau, 2015; Zilioli & Bird, 2017), paving the way for future comparative studies on the evolution of endocrinological mechanisms (see, for instance, Ostner, Heistermann, & Schülke, 2011, for a study on androgens and aggressiveness in a nonhuman primate species; and Muller & Wrangham, 2004, for evidence on acute T increases in a mating context in chimpanzees). There already are studies on mechanisms of sexual selection in nonhuman primates (e.g., Clutton-Brock, 2007; Kappeler & van Schaik, 2004; Soltis et al., 1997), showing that both male-male competition and female mate choice, but also scrambles and sexual coercion, are influential (see also Puts, 2016). As Zilioli and Bird (2017) suggested that T reactivity may be adaptive, it would be interesting to examine associations with mating success for a functional analysis. We do have T reactivity measures in our sample (see Manuscript 1), which we initially did not include in Manuscript 2 to reduce the study's complexity and because we focussed on men's trait rather than state variables. Including both *post*-T reactivity measures in (separate) structural equation models (besides the other five traits, see above) and also investigating bivariate correlations (between T reactivity and all mating success measures), we found no significant effects whatsoever, neither on female mate choice, male-male competition nor mating success (see Tables S2 and S3). We hence do not provide support for competition-induced T reactivity having an "evolved function" (in the terminology of Tooby, Cosmides, Sell, Lieberman, & Sznycer, 2008, p. 252). Thus, whereas in Manuscript 1 we show some influence of T reactivity in men's competitive behaviour, also regarding associations with personality state changes, in Manuscript 2 we found no direct evidence for either baseline T or T reactivity as an underlying mechanism in sexual selection on men. Still, it remains possible that rather than current baseline T levels, pubertal and/or perinatal T levels may be more relevant in this context (e.g., Whitehouse et al., 2015), due to developmental links with traits implicated in sexual selection (Hill, Bailey, & Puts, 2017), like physical strength (Lassek & Gaulin, 2009). Alternatively, one may find associations with baseline T or T reactivity, when directly measuring reproductive success or evolutionary fitness, rather than mating success. A final possibility is that effects are undermined by hidden moderators or mediators, such as genetic variables. Previous studies have shown the CAG repeat length of the androgen receptor gene to modulate phenotypic traits in men (Simmons & Roney, 2011), like physical strength and dominance, which were also found to be influential in the study in Manuscript 2, and to predict T responses in men after interacting with a woman (Roney, Simmons, & Lukaszewski, 2010). Consequently, future research may set out to examine further inter-individual differences moderating and/or mediating the role of hormonal variables in sexual selection on men.

As a final important aspect, the findings regarding hormonal reactivity are only correlational, and to gain insights into causal effects, the setting of Manuscript 1 could be enriched by a T administration design (McCall & Singer, 2012). Subsequent personality state changes, both self-reported and observer-rated, could be investigated, to determine whether T reactivity has got any causal influence on competition-related personality changes and social signalling.

Conclusion

Male competition for resources such as mates, status and territory is ubiquitous in human evolution. In this dissertation, different facets of men's competitive behaviour, including endocrinological, personality psychological and sexual selection aspects, were investigated. Manuscript 1 examined the interplay of acute hormonal reactivity and personality state changes, the latter both reported by the male participants themselves and perceived by unacquainted observers, after engaging in an intrasexually competitive situation. Our main findings of an acute testosterone response and associated increases in self-reported competitiveness, as well as observer-perceived dominance and self-assurance (partly attenuated by high baseline cortisol) indicate that hormonal reactivity and personality state changes may be functional in life history trade-offs and facilitate competitive behaviour and social signalling to both male rivals and potential female mates. In Manuscript 2, we focussed on the role of men's sexually dimorphic traits in relation to the two primary mechanisms of sexual selection, male-male competition and female mate choice. It appeared that men's formidable traits, especially physical strength and upper body size, enhanced their access to females and increased their mating success by intimidating and competing with other males, rather than by directly being perceived as attractive and chosen by females. This dissertation suggests an abundance of future research pathways to study human competitive behaviour for further insights into men's life history and sexual selection.

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7. Supplementary material

Table S1

Bivariate correlations between testosterone reactivity and circumplex personality traits

	1st T reactivity		2nd T reactivity	
Personality trait	*r*	*p*	*r*	*p*
Dominance (PA)	.04	.69	-.04	.67
Competitiveness (BC)	.10	.25	.06	.54
Coldheartedness (DE)	.12	.18	.00	.99
Introversion (FG)	.15	.10	.02	.86
Submissiveness (HI)	-.02	.79	.07	.47
Ingenuousness (JK)	-.06	.51	-.03	.76
Warmth (LM)	-.06	.53	.08	.38
Extraversion(NO)	-.03	.71	.14	.12

Note: 1st/2nd T reactivity = 1st/2nd testosterone reactivity *post*-measure; experimental group only (*n* = 124).

Table S2

Effects of testosterone reactivity on physical dominance and sexual attractiveness in the structural equation models

	Physical dominance				Sexual attractiveness			
	1st *post*-sample		2nd *post*-sample		1st *post*-sample		2nd *post*-sample	
T1	*β*	*p*	*β*	*p*	*β*	*p*	*β*	*p*
sociosexual behaviour	-.05	.44	.01	.87	.01	.94	.09	.19
sexual partners 12 m.	-.05	.44	.01	.88	.01	.94	.09	.20
T2								
sociosexual behaviour	-.05	.41	.01	.87	.00	.97	.09	.19
sexual partners 12 m.	-.05	.41	.01	.87	.00	.96	.09	.19
NPCs	-.05	.41	.02	.86	.00	.96	.09	.19

Note: 1st/2nd T reactivity = 1st/2nd testosterone reactivity *post*-measure; T1/T2 = time point 1/2; sexual partners 12 m. = number of sexual partners within the previous 12 months; NPCs = number of potential conceptions.

Table S3

Bivariate correlations between testosterone reactivity and mating success measures

	1st T reactivity		2nd T reactivity	
T1	*r*	*p*	*r*	*p*
sociosexual behaviour	-.02	.82	-.04	.57
sexual partners 12 m.	.02	.84	.01	.85
T2				
sociosexual behaviour	-.17	.08	-.06	.52
sexual partners 12 m.	-.08	.43	.04	.69
NPCs	-.11	.28	-.01	.93

Note: 1st/2nd T reactivity = 1st/2nd testosterone reactivity *post*-measure; T1/T2 = time point 1/2; sexual partners 12 m. = number of sexual partners within the previous 12 months; NPCs = number of potential conceptions.

Appendix A – Acknowledgements part II

Nun möchte ich ausführen, wofür ich euch dankbar bin. Diese Liste ist nicht geordnet und natürlich nicht exhaustiv; auf manche Personen trifft bestimmt mehr als ein Punkt zu. Ich hoffe, dass ihr euch jeweils an den richtigen Stellen angesprochen fühlt - bei Zweifeln und Fragen versuche ich gerne aufzuklären.

Ich danke euch/dir …

dass ich sehr viel von dir lernen konnte, sowohl über die wissenschaftliche Forschung allgemein, als auch über die Biologische Persönlichkeitspsychologie speziell.

für eure Bereitschaft, meinem Promotionskomitee anzugehören und der Disputation beizuwohnen, und somit dieses Dissertationsprojekt formell „abzurunden".

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für die besten Mitternachts-Probanden, und einige lustige gemeinsame Stunden in Göttingen.

für Nachsicht, einen (wissenschaftlichen) Fehler zu verzeihen, sowie die Energie diesen zu korrigieren und das Projekt auf eine letztendlich erfolgreiche Art zu retten.

für spitzenmäßige Rückmeldungen und Verbesserungsvorschläge des „Mantels" meiner Dissertation – ihr habt mir sehr geholfen, diesen verständlicher und klarer zu formulieren (und natürlich etliche Flüchtigkeitsfehler zu vermeiden).

für die beste „attraktive weibliche Konföderierte".

für die Vermittlung von Werten wie Demut, Bescheidenheit, Optimismus, Selbstvertrauen, Gründlichkeit und Offenheit.

für die stetige Ermunterung, an mich zu glauben und meinen Fähigkeiten zu vertrauen.

für gelegentliche kleine notwendige „Stupser“, Neues auszuprobieren und die Komfortzone zu verlassen, außerhalb derer man oft Neues lernen und sich selbst neu entdecken kann.

für Liebe, Aufmerksamkeit, vielerlei Unterstützung, auch in schwierigen Zeiten.

dass ich euch mit viel Freude betreuen durfte und wir zusammen an doch teilweise ambitionierten Projekten arbeiten durften - ich hoffe, sie tragen bald auch über diese Dissertation hinaus Früchte.

für große materielle Unterstützung während der Promotion, sowie vielfältige Möglichkeiten, in der Lehre zu lernen und reifen, und auf bereichernden Konferenzen unsere Forschung zu präsentieren.

für Motivation und Anregung während meiner Studien in Groningen und Oxford.

für Debatten über Themen der Psychologie und darüber hinaus.

für Ausgleich und Ablenkung neben den oft sehr langen Bürostunden.

für fleißige und zuverlässige Hilfe bei teilweise großen und aufwändigen Datenerhebungen.

für viele schöne Momente, Liebe, Verlässlichkeit, Wärme, Sinn, Aufmerksamkeit und Aufmunterung.

für exzellentes Feedback, welches gelegentlich reifte wie guter Wein, nur um dann noch besser zu werden als dieser.

für entspannende Yoga-Stunden unter der Aufsicht von 12 Kameras (die hoffentlich währenddessen ausgeschaltet waren).

für die Bereitschaft, in einer zeitkritischen Phase deinen Artikel hintenanzustellen.

für auflockernde, witzige Gespräche, die dem „Büroalltag“ Farbe geschenkt haben.

dass ich mit euch viel lernen, erleben und Spaß haben durfte.

für eine grandiose Zeit in Groningen.

für eine wundervolle und beeindruckende Zeit in Oxford.

für „Necessito gasolina para mi jetski”, und so viel mehr Spaß und Lebensfreue.

dass du mich zu deinem Partner gewählt hast - ich weiß nicht, ob das eher meiner fragwürdigen *sexual attractiveness* oder begrenzten *physical dominance* zuzuschreiben ist; mit dir habe ich aber zweifelsohne einen äußerst hohen (qualitativen) *mating success* erlangt. Jedes Mal, wenn ich dich sehe, schießt mein *testosterone* in die Höhe, und meine *personality states* spielen verrückt. Und wer weiß, vielleicht führen unsere gemeinsamen *potential conceptions* ja irgendwann einmal zu einer echten *conception*. Würde mich freuen.

Appendix B – Curriculum Vitae

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Education

University of Göttingen, Georg-Elias-Müller Institute for Psychology 2014 -
Biological Personality Psychology (Prof. Lars Penke)
PhD programme "Behaviour and Cognition"
Doctorate studies on "Intra- and Intersexual Selection on Men: Their Relative Importance and Hormonal Underpinnings"
Advisors: Prof. Lars Penke, Prof. Mitja Back, Prof. Julia Ostner

University of Oxford, Institute of Cognitive and Evolutionary Anthropology (UK) 2012 - 2013
M.Sc. Cognitive and Evolutionary Anthropology
M.Sc. dissertation: "A face to be reckoned with: the relationship between facial, psychological and behavioural dominance"
Supervisor: Dr. Oliver Curry

University of Groningen, Faculty of Behavioural and Social Sciences (Netherlands) 2009 - 2012
B.Sc. Psychology (taught in English) – completed *cum laude*
B.Sc. thesis: "Tall claims? The relationship between height and dominance"
Supervisor: Dr. Gert Stulp
2nd year: Excellence Programme (research internship, thematic meetings, theoretical seminar, research seminar)

University of Bremen 2008 - 2009
Mathematics

Goethe-Gymnasium Ibbenbüren 1998 - 2007
A-Levels

Publications

Kordsmeyer, T. & Penke, L. (submitted). The relative importance of intra- and intersexual selection on human male sexually dimorphic traits.

Kordsmeyer, T. & Penke, L. (under review). Effects of male testosterone and its interaction with cortisol on self- and observer-rated personality states in a competitive mating context.

von Borell, C., Kordsmeyer, T., Gerlach, T. M., & Penke, L. (under review). An integrative study of facultative personality calibration.

Kordsmeyer, T., & Penke, L. (2017). The association of three indicators of developmental instability with mating success in humans. *Evolution and Human Behavior, 38*, 704-713.

Kordsmeyer, T. L., MacCarron, P., & Dunbar, R.I.M. (2017). Sizes of permanent campsite communities reflect constraints on natural human communities. *Current Anthropology, 58*, 289-294.

Stulp, G., Kordsmeyer, T., Buunk, A.P., & Verhulst, S. (2012). Increased aggression during human group contests when competitive ability is more similar. *Biology Letters, 8,* 921-923.

Conference presentations

Kordsmeyer, T., & Penke, L. (2017, September). *Effects of male testosterone and cortisol reactivity on self-and observer-rated personality in a competitive mating context.* Paper presented at the 15th annual meeting of the German Society for Psychology's (DGPs) Unit for Differential and Personality Psychology and Psychological Diagnostics (DPPD), Munich, Germany.

Kordsmeyer, T., & Penke, L. (2017, June). *Effects of male testosterone and cortisol reactivity on self-and observer-rated personality in a competitive mating context.* Paper presented at the 29th HBES conference, Boise, Idaho.

Kordsmeyer, T. & Penke, L. (2017, April). *The relative importance of various attractiveness and dominance measures in sexual selection on human males.* Poster presented at the EHBEA 2017 conference, Paris, France.

Kordsmeyer, T., & Penke, L. (2016, September). *Effects of male testosterone and cortisol reactivity on self- and observer-rated personality in an intrasexual competition context.* Paper presented at the 50th annual meeting of the German Society for Psychology (DGPs), Leipzig, Germany.

Kordsmeyer, T., & Penke, L. (2016, July). *Effects of male testosterone and cortisol reactivity on self- and observer-rated personality in a competitive mating context.* Paper presented at the 18th ECP conference, Timisoara, Romania.

Kordsmeyer, T., & Penke, L. (2016, April). *Effects of male testosterone and cortisol reactivity on self-and observer-rated personality states in a competitive mating context.* Poster presented at the EHBEA 2016 conference, London, UK.

Kordsmeyer, T., Jünger, J., & Penke, L. (2016, April). *Psychological-anthropological studies using a 3D body scanner.* Talk presented at the Anwenderforum Bodyscanning, HumanSolutions, Kaiserslautern, Germany.

Kordsmeyer, T., & Penke, L. (2015, September). *Self-perceived personality plasticity in men in a intrasexual competition context.* Paper presented at the 13th annual meeting of the German Society for Psychology's (DGPs) Unit for Differential and Personality Psychology and Psychological Diagnostics (DPPD), Mainz, Germany.

Kordsmeyer, T., & Penke, L. (2015, June). *Effects of male testosterone and cortisol reactivity on self- and observer-rated personality in the mating context.* Poster presented at the Adaptive Human Behavior and Physiology Workshop, Erice, Italy.

Kordsmeyer, T., & Penke, L. (2015, May). *Sexual selection for symmetry: Three indicators of developmental instability in relation to mating success in humans.* Paper presented at the 27th HBES annual meeting, Columbia, Missouri.

Kordsmeyer, T., & Penke, L. (2015, February). *Sexual selection for symmetry: Three indicators of developmental instability in relation to mating success in humans.* Poster presented at the GOEvol meeting, Göttingen, Germany.

Grants/scholarships (overall ~29.200 €)

Travel grant for research stay at the University of Tokyo, Japan 12/2017
Leibniz-ScienceCampus "Primate Cognition" (LSC), University of Göttingen, 2.465 €

Travel grant for a conference visit 06/2017
Leibniz-ScienceCampus "Primate Cognition" (LSC), University of Göttingen, 1.000 €

Travel grant for a conference visit 04/2017
Göttingen International grant for EHBEA 2017, 320,60 €

Travel grant for a conference visit 07/2016
German Academic Exchange Service (DAAD) grant for ECP18, 702 €

LSC Seed Fund for a research project with Prof. Penke and Prof. Ostner 06/2016 - 05/2017
Leibniz-ScienceCampus "Primate Cognition" (LSC), University of Göttingen, 9.947,80 €

Travel grant for a conference visit 04/2016
Student bursary for EHBEA 2016, 100 €

Travel grant for a conference visit 04/2016
Göttingen International conference grant for EHBEA 2016, 414 €

Travel grant for a conference visit 05/2015
Leibniz-ScienceCampus "Primate Cognition" (LSC), University of Göttingen, 1.000 €

Travel reimbursement for a conference visit 05/2015
Human Behavior and Evolution Society, US-$300

1-year scholarship for M.Sc. at Oxford 10/2012 - 08/2013
German Academic Exchange Service ('DAAD'), approx. 13.000 €

Teaching experience

Georg-Elias-Müller-Institute of Psychology, University of Göttingen 11/2017 - 12/2017
2nd-year Psychology B.Sc. seminar, 'Test theory'

Private University of Applied Sciences Göttingen (PFH) 10/2016 - 09/2017
1st-year Psychology M.Sc. seminar, 'Psychological diagnostics'

Georg-Elias-Müller-Institute of Psychology, University of Göttingen 10/2016 - 03/2017
2nd-year Psychology B.Sc. seminar, 'Test theory'

Georg-Elias-Müller-Institute of Psychology, University of Göttingen 04/2016 - 10/2016
2nd-year Psychology B.Sc. seminar, 'Personality psychology', esp. 'Hormones & personality'

Georg-Elias-Müller-Institute of Psychology, University of Göttingen 10/2015 - 03/2016
2nd-year Psychology B.Sc. seminar, 'Test theory'

Georg-Elias-Müller-Institute of Psychology, University of Göttingen 04/2015 - 02/2016
Supervising two Master's theses (Psychology M.Sc.)

Georg-Elias-Müller-Institute of Psychology, University of Göttingen 04/2015 - 09/2015
2nd-year Psychology B.Sc. seminar, 'Behavioural observation & interview methods'

Faculty of Behavioural and Social Sciences, University of Groningen 01/2012 - 07/2012
1st-year Psychology B.Sc. course, 'Intervention & dialogue' (taught in English)

Ad-hoc reviewer

European Journal of Personality, Frontiers in Psychology

Working experience

Georg-Elias-Müller-Institute of Psychology, University of Göttingen 10/2014 -
Lab manager, scientific staff (Dept. of Biological Personality Psychology)

Rocket Internet, Berlin 10/2013 - 04/2014
Internship in Human Resources

Professional affiliations

Human Behavior & Evolution Society (HBES), European Human Behaviour and Evolution Association (EHBEA), Leibniz-ScienceCampus (LSC), PhD Programme "Behavior and Cognition" (BeCog), German Society for Psychology (DGPs) – Unit for Differential and Personality Psychology and Psychological Diagnostics (DPPD), Göttingen Open Science and Source Initiative of Psychology (GOSSIP)

Additional skills

IT skills
R, SPSS, Microsoft Office

Languages
German (mother tongue), English (fluent in text and speech), Latin (from school), Dutch (basic knowledge)

Göttingen, December 19th, 2017

Tobias Kordsmeyer