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Review Article

A review of human male field studies of hormones and behavioral reproductive effort☆

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ABSTRACT

The purpose of this paper is to review field studies of human male hormones and reproductive behavior. We first discuss life history theory and related conceptual considerations. As illustrations, distinctive features of human male life histories such as coalitional aggression, long-term partnering and paternal care are noted, along with their relevance to overall reproductive effort and developmental plasticity. We address broad questions about what constitutes a human male field study of hormones and behavior, including the kinds of hormone and behavioral measures employed in existing studies. Turning to several sections of empirical review, we present and discuss evidence for links between prenatal and juvenile androgens and sexual attraction and aggression. This includes the proposal that adrenal androgens—DHEA and androstenedione—may play functional roles during juvenility as part of a life-stage specific system. We next review studies of adult male testosterone responses to competition, with these studies emphasizing men's involvement in individual and team sports. These studies show that men's testosterone responses differ with respect to variables such as playing home/away, winning/losing, and motivation. Field studies of human male hormones and sexual behavior also focus on testosterone, showing some evidence of patterned changes in men's testosterone to sexual activity. Moreover, life stage-specific changes in male androgens may structure age-related differences in sexual behavior, including decreases in sexual behavior with senescence. We overview the considerable body of research on male testosterone, partnerships and paternal care, noting the variation in social context and refinements in research design. A few field studies provide insight into relationships between partnering and paternal behavior and prolactin, oxytocin, and vasopressin. In the third section of the review, we discuss patterns, limitations and directions for future research. This includes discussion of conceptual and methodological issues future research might consider as well as opportunities for contributions in under-researched male life stages (juvenility, senescence) and hormones (e.g., vasopressin).

Contents

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1. Introduction

The aim of this paper is to critically review field studies of human male hormones and reproductive behavior. We also seek to situate this effort within the themes of other contributions of this special edition of "Hormones and Behavior." Toward these ends, we first consider human life histories. This entails discussion of the similarities and differences of human life histories with those of other animals, along with key concepts such as the inter-twining of proximate hormone mechanisms and development with ultimate adaptive and phylogenetic considerations. We next review human male field studies on hormones and behavioral reproductive effort. This includes sections on children and adults, and attends to key behavioral domains of sexuality, physical aggression and competition, and the formation of long-term romantic partnerships and paternal care. The array of field studies covers indicators of perinatal androgen exposure (e.g., 2D:4D), sexual differentiation of external genitalia and psychosexual orientation, a small number of studies on prepubescent boys' reproductive endocrinology and social behavior, a sizable literature on adult male hormonal responses to athletic competition, studies on male hormonal responses to courtship and sexual behavior, and data on hormones and men's involvement in long-term romantic partnerships and paternal behavior. The third section of this paper identifies patterns, limitations, and directions for future research in field studies of human male reproductive behavior. Contrasts in the methods with other taxa, particularly nonhuman primates, are discussed. We address considerations such as the challenges of behavioral measurements and hormonal correlates, the opportunities afforded to reach large samples of variable developmental experience, and the inordinate prospects for novel contributions in focusing on pre-pubescent and senescing human male samples.

2. Part I. Life history theory

Life history theory recognizes that organisms adaptively allocate their limited time and resources to maximize relative reproductive success (Stearns, 1992). Allocations are devoted to growth, maintenance and reproduction, the latter of which is our focus in this paper. Hormonal systems play key mechanistic roles in coordinating adaptive life history allocations at various timescales (Adkins-Regan, 2005; Del Giudice et al., 2015; Muehlenbein and Flinn, 2011). These include acute (short-term) hormone changes in response to various reproductive challenges, such as male-male competition, as well as regulating major developmental transitions across the life course, such as adrenarche (rise of adrenal androgens in mid-childhood) and puberty. Species, populations and individuals vary in their life history allocation to reproductive effort (Del Giudice et al., 2015; Muehlenbein, 2010; Stearns, 1992). Species or broader phylogenetic distinctions in life histories (patterns in allocations to growth, maintenance and reproduction across the life course, as measured by variables such as age of weaning, sexual maturity and reproductive scheduling) emphasize the role of evolutionary history and adaptation. Population and individual differences in life histories can be traced, in part, to genetic differences (Day et al., 2016; Johnson et al., 2009; Stearns, 1992), though most of the focus here and generally in human behavioral endocrinology is on development and plasticity (e.g., the impacts of social and other cues at specific life stages that bear upon an organism's subsequent hormones and behavior).

As a species, humans evolved in sub-Saharan Africa approximately 150,000 years ago (Tattersall, 2012). Since around 70,000 years ago, a relatively small population of modern humans spread outside of Africa, with some small degree of interbreeding with Neandertals and Denisovans, to give rise to more than 7 billion humans present today (Green et al., 2010; Harcourt, 2012; Reich et al., 2010). Through these dramatic global migrations, humans have faced and created variable socioecologies. This includes variable rates of individual and coalitional physical aggression, number of sexual partners, expectations of courtship, and variation in partnering and paternal roles (Bribiescas et al., 2012; Gray and Garcia, 2013; Henrich, 2015; Kaplan et al., 2009; Marlowe, 2000). That plasticity—part of our species' cross-cultural and historic variation—warrants direct attention in field studies of male hormones and behavioral reproductive effort.

How do human life histories compare with those of other animals? Like other great apes, humans have long gestation, extended childhood, late age of puberty and long lifespan compared with the Asian and African monkeys from which apes and humans evolved (Kappeler and Pereira, 2003; Mitani et al., 2012). That said, humans also differ from our closet ape kin in several facets of life history, including ones germane to this review: extended postnatal brain growth, later age of puberty, relatively higher fertility, paternal involvement, and extended lifespan (e.g., Kaplan et al., 2000; Robson and Wood, 2008). The adaptive causes of derived human life history features are outside the scope of this paper. Yet, the existence of an extended childhood provides opportunities for honing valuable social competencies in navigating complex male-male alliances and competition (Flinn, 1997; Humphrey, 1976; Konner, 2010), and the existence of extended lifespans allows older males to continue seeking mates, engaging in political behavior, and providing care and resources to descendant kin (Bribiescas, 2016; Simmons, 1970), all of which may have hormonal substrates that have barely attracted attention. Unlike our closest living relatives, chimpanzees and bonobos, human males also tend to reproduce within long-term sociosexual bonds and provide parental care (Gray, 2013; Gray and Anderson, 2010; Wrangham and Peterson, 1997), facets of male reproductive behavior that have been the focus of hormones and behavior field studies noted below.

Hormones both bias and respond to human male reproductive behavior, as is the case in other animals (Adkins-Regan, 2005; Gettler, 2014; Nelson, 2011). Perhaps the earliest of human "field" studies of hormones and male reproduction involved castration (Wilson and Roehrborn, 2000). Eunuchs (castrated males) are regularly discussed in the Old Testament of the Bible, reference to a past time in which they were more common in socially unequal despotic societies. A more recent historic studies of Korean male eunuchs showed that castrated males tended to live longer lives than intact controls (Min et al., 2012). These human eunuch studies point to potential links between testosterone and life history outcomes as well as a causal role of testosterone on male reproductive performance. Some hormones such as testosterone may favor behaviors enhancing reproductive success rather than maintenance, which leads to the recognition of potential tradeoffs (mutually exclusive outcomes) in life history allocations (Bribiescas, 2001; Ellison, 2003; Ellison and Gray, 2009; Wingfield et al., 2001). In this vein, resources spent on reproductive behavior are not available for growth or maintenance; and time devoted to mating effort (male-male competition, courtship, sexual coercion) is not available for certain forms of paternal effort such as direct childcare of dependent offspring.

Experimental work (whether castration or in hormone administration studies) can demonstrate the effects of hormones on behavior. However, nearly all of the field studies we review test the effects of a male social behavior on hormones. The observation that behaviors influence hormones has several important facets. One is that this raises the question of how (e.g., mechanism) and why (e.g., potential adaptive and functional significance) this happens. Primarily lab-based studies suggest that the hormone responses to a behavior can shape subsequent behavior, including with respect to increasing competitive motivation (Mehta and Josephs, 2006) and aggressive behavior (Carré et al., 2013). Such studies suggest that some of these differing hormonal responses may adaptively modulate future behavioral responses to subsequent competitive encounters, such as promoting avoidance behavior following a defeat, or increasing the likelihood of engaging in further competitive behavior following a victory. However, it is important to note that these studies are correlational, and the extent to which such hormonal fluctuations play a causal role in shaping human social

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behavior will require experimental approaches (e.g., pharmacological challenge).

As in the field of hormones and behavior generally, any specific study must be put in socioecological context and in light of life history considerations (Adkins-Regan, 2005; Ellison and Gray, 2009). While there may be heritable, species-specific, population-specific and individual-specific propensities for certain hormone-behavior relationships, how these play out is always contingent upon socioecological and life history considerations. The nature of potential tradeoffs between male aggression and direct childcare is specific to socioecological context, with males in some cases putting virtually all of their behavioral reproductive effort into mating effort (aggression) rather than parenting effort, while in other cases the opposite holds. The key is to situate hypotheses concerning male hormones and behavior in field studies within specific features of the relevant socioecology.

Furthermore, any aspect of male hormones and behavior is contingent upon heritable genetic, developmental and current factors. While one might posit that male testosterone levels will increase in response to physical competition, this may be dependent upon the individual's life stage (e.g., early adulthood vs. late adulthood), health status, genetic background (perhaps variations in how the androgen receptor differentially bind and thus induce differential effects of a given increase in testosterone), and how one's childhood influenced a perception of the meaning of that competition. Any behavior is also dependent upon other bodily systems such as those involved in growth (e.g., growth hormones and IGF-1) and maintenance (e.g., immune function, gut microbiota). These of course cannot all be controlled for in any field study. Importantly, if adequate time and resources exist within individuals or even populations, then tradeoffs postulated on the basis of scarcity may not apply. This is akin to the idea that if some individuals or populations have a larger energetic pie then they can devote more to growth, reproduction and maintenance rather than face challenging allocation tradeoffs. This conceptual issue plagues human field studies of hormones and behavior, and thus warrants close scrutiny of ways to try addressing it such as through use of key covariates.

3. Part II. Review of field research

Given that the focus of this review paper is on field studies documenting human male hormones and reproductive behavior, what kinds of studies does this encompass? The empirical studies we feature often have a hormone measure (e.g., urinary oxytocin concentration) and a behavioral measure (e.g., participation in a naturalistic athletic competition) obtained from a non-lab setting. However, there are also some variations upon these criteria in the studies we assess.

We largely draw upon studies employing minimally invasive sample collection of hormone concentrations, which in practice emphasizes saliva and to lesser degrees urine and finger prick blood spots. The use of minimally invasive sample collection has advantages of feasibility (more participants willing to provide such samples), expense (avoiding the cost of a phlebotomist drawing blood samples, for example) and ecological relevance (can be obtained in ongoing activities without inducing a physiological stress response). However, different media are also differentially useful for measuring different hormones (e.g., a salivary vasopressin assay has not, to our knowledge, been regularly used or validated, and cerebrospinal fluid measures of oxytocin are not amenable to field studies) and with respect to other considerations such as time integration and frequency of sampling (e.g., urine samples integrate hormone concentrations over longer periods of time, but can be obtained less frequently than finger pricks or saliva samples). Other references discuss these kinds of considerations in greater depth (e.g., Anestis, 2010; McDade et al., 2007; Saxbe, 2008; van Anders et al., 2014a, 2014b), and we also touch on related methodological points at appropriate places below. We also occasionally refer to a study that uses a different proxy for hormone measurement. Studies of 2D:4D provide a crude index of perinatal androgen exposure (McIntyre, 2006), which can be useful in studies seeking to address purported perinatal organizing effects of androgens on human male reproductive behavior. In a few cases, a subject's age (e.g., age 8, preceding puberty) serves an indirect proxy of hormone status, in this case with respect to the typical adrenal androgen exposure associated with adrenarche, mid-childhood activation of the adrenal gland that is characterized by an increase in release of adrenal androgens such as dehydroepiandrosterone (DHEA) (Campbell, 2006).

Behavioral measures in the field also show some methodological variation in the studies we review (Martin et al., 1993). Many rely on naturalistic study designs, enabling measurement of behaviors in everyday kinds of behaviors, such as paternal care or individual or team sports competition. Advantages of these naturalistic methods are ecological validity and more ready parallels with behavior of nonhuman animal field studies (e.g., winner/loser effects, home versus away competition). However, behavior in human male field studies can be assessed in other ways, including self-report in interviews or questionnaires, during tech-facilitated interfaces in naturalistic contexts (e.g., beeper studies, in which a male records his behavior at specific times), and behavioral observation (e.g., teacher or parental reports of a child's behavior at school or at home), among other leading behavioral methods. Some of these methods blur the lines of a field assessment of behavior. Does a male participant answering questions about his sexual or paternal behavior in a home interview count as a field study? What about that same participant answering the same questions in a clinical setting or social psychology lab? The measure may refer to naturalistic behavior, but was not necessarily obtained in the field. All said, we share these methodological considerations about the scope of field studies at the beginning of this empirical portion of the review in order to highlight our emphasis on field studies but also mindful of some gray areas. Moreover, we sometimes refer to lab or clinical studies if these offer complementary insights (e.g, with respect to causality or mechanism) that might be otherwise difficult to do among field studies. Finally, to provide an empirical roadmap of the field studies terrain we cover in this review, Fig. 1 highlights the key behavioral categories and relationships to hormones that we now address.

3.1. Field studies of prepubescent males' reproductive endocrinology

Although a role for hormones during early development has been established using animal models and clinical populations, most research that has investigated male reproductive endocrinology in field studies is limited to adolescents and adults of prime reproductive age. This section reviews field studies that focus on organizational and activational effects of gonadal and adrenal androgens in the context of prepubescent boys' reproductive behaviors. Organizational effects of androgens permanently regulate the trajectory of reproductive behavioral neural circuitry, along with other physiological systems, during critical developmental periods (Berenbaum and Beltz, 2011) (Fig. 2). In contrast, activational effects of androgens happen later in life and tend to be acute and temporary changes that impact brain, energy metabolism, and behavior (Cohen-Bendahan et al., 2005). For our purposes, reproductive behaviors in boys include male sex-type play behaviors, sexual attraction and sexual arousal toward others, and physical male-male competition and aggression. The evidence suggests that prenatal androgen hormone exposure has a significant role in influencing the development of external genitalia, gender identity, heterosexual preference, and male sex-typed interests in childhood (e.g., Auyeung et al., 2009; Herdt and Davidson, 1988; Hönekopp and Thierfelder, 2009; Imperato-McGinley et al., 1974). Additionally, field studies which have investigated the interaction between endocrine processes that are specific to childhood development, such as adrenarche, and emergent reproductive behaviors are discussed (e.g., Herdt and McClintock, 2000; McHale et al., 2016). Findings are situated within a life history framework, with considerations given to endocrine responses that may differ across the life course.

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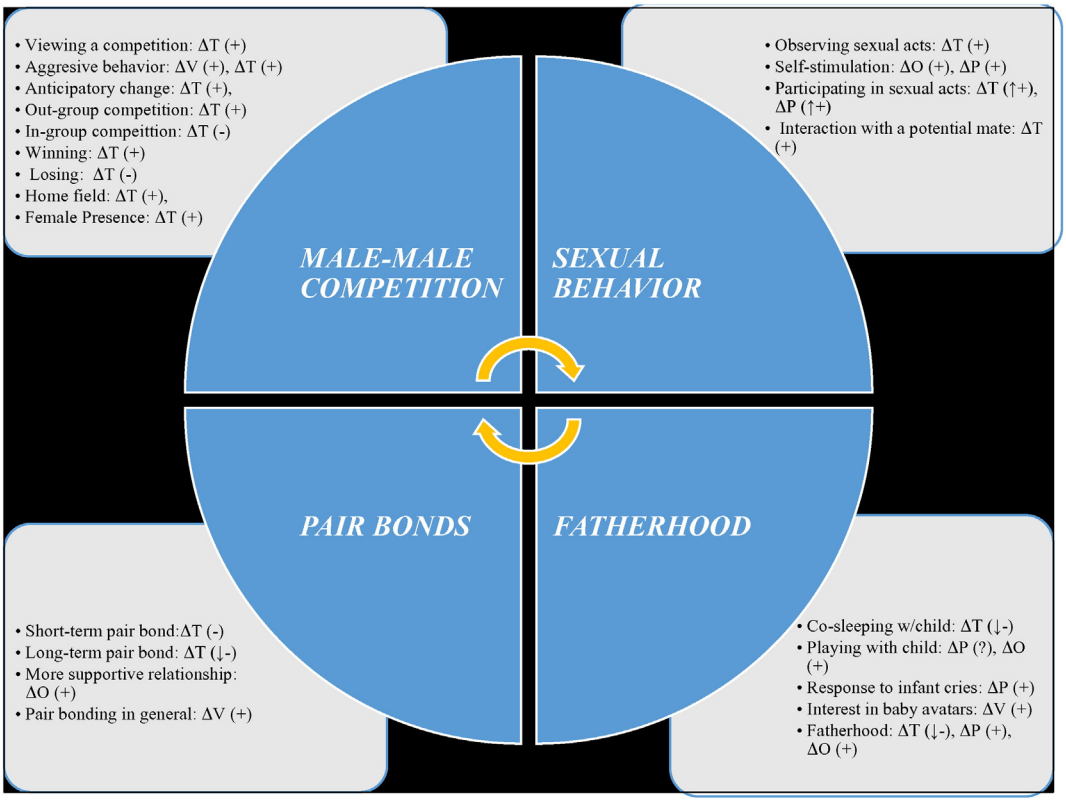

Fig. 1. Reproductive Behavioral Domains and Hypothesized Adult Male Hormone Responses for change in testosterone (ΔT), vasopressin (ΔV), prolactin, (ΔP), and oxytocin (ΔO). Positive (+) signifies increase. Negative (−) signifies decrease. Downward arrow (↓) signifies "greater decrease." Upwards arrow (↑) signifies "greater increase." Question mark (?) signifies mixed results.

Several field studies have provided valuable insights to the understanding of the influences of early androgen exposure on sexual differentiation of external genitalia and psychosexual orientation. A classic study conducted in the Dominican Republic community of Las Salinas was one of the first to report on the high incidence of a rare autosomal genetic disorder known as 5-alpha reductase deficiency (Imperato-McGinley et al., 1974). The 5-alpha reductase enzyme is responsible for converting testosterone into dihydrotestosterone during normal fetal development, an essential step that leads to the masculinization of the male external genitalia in utero (Imperato-McGinley et al., 1974). Twenty-four males from 13 families were reported to express androgen deficiency within this community (Imperato-McGinley et al., 1974). These individuals are born with female-like external genitalia (i.e. a bifid scrotum that looks like labia), possess normal to high

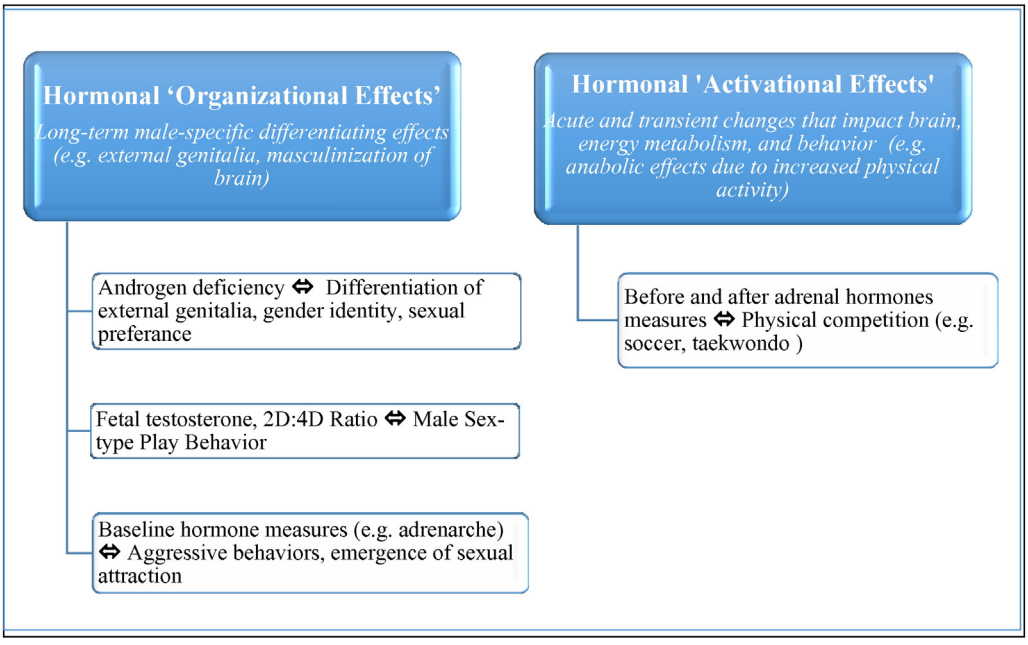

Fig. 2. Field studies investigating organizational and activation effects impacting boys' reproductive endocrinology and behavior.

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levels of testosterone, and lower than normal levels of dihydrotestosterone during childhood (Imperato-McGinley et al., 1974). The masculinization of the male genitalia does not occur until puberty, at which time the testes and penis develop externally. Interestingly, parents often assigned and raised these children as girls until normal sexual differentiation occurs at puberty. In spite of possessing ambiguous external genitalia and being raised as girls from birth, nearly all of the individuals surveyed report having strong heterosexual preferences and identify as male. Similar findings were reported among the Sambia tribe of Papua New Guinea in addition to the people of the Taurus Mountains of southern Turkey, such that male identity and heterosexual preference best characterizes those individuals who express 5-alpha-reductase deficiency (Akgun et al., 1986; Herdt and Davidson, 1988). Thus, normal to high levels of prenatal testosterone exposure appears sufficient to influence the formation of a male gender identity and heterosexual preference. These cross-cultural findings speak to the organizational effects of prenatal androgens on sexual differentiation of external genitalia and gender development and sexual preference.

Evidence from studies utilizing direct (e.g., amniotic fluid) and indirect (e.g., 2D:4D ratio or anogenital distance) measures of prenatal androgen exposure lend further support to the view that androgens also play a role in masculinizing boys' sex-typed play behavior. Auyeung et al. (2009) assessed the relationship between fetal testosterone in amniotic fluid from pregnant women and subsequent sex-typed behavior in 112 boys, aged 6–10 years from Cambridge, United Kingdom. The Pre-School Activities Inventory (PSAI) was filled out by a parent and used to score their child's characteristics and toy and activity preferences, where higher scores relate to more male-typical behaviors. The results from the study found a significant positive correlation between fetal testosterone and PSAI scores in boys, supporting an organizational role of the fetal environment in directing the expression of boys' sex-typed behavioral phenotypes. Given the limitation of having to extract amniotic fluid in a medical setting, this research is not considered a traditional field study. It nonetheless complements the research discussed previously because it examined the relationship between boys' play behaviors in an everyday context (as reported by the mother) with a prenatal hormonal correlate. Similar results were also found using indirect hormone measures to assess prenatal hormone exposure. A study conducted on 95 German pre-school boys, aged 1.9 to 5.6 years, analyzed the relationships between digit ratios (2D:4D) and PSAI scores (Hönekopp and Thierfelder, 2009). Previous reports indicate that 2D:4D is negatively correlated with early testosterone exposure (e.g., Manning et al., 1998; Manning et al., 2007; Trivers et al., 2006). Hönekopp and Thierfelder (2009) found a significant negative correlation between 2D:4D ratio of the left hand and male-typical play behavior, but not in the right hand. The results from the aforementioned studies suggest that direct and indirect hormonal correlates can be used to assess the masculinizing effects of androgens on boys' play behavior across early and middle childhood. However, Wong and Hines (2016) conducted a similar study on 2–3 year old boys' 2D:4D and sex-type behavioral measures and found only partial support for the previous findings reported by Hönekopp and Thierfelder (2009). Wong and Hines (2016) report that 2D:4D was negatively correlated with PSAI score in the right hand only and it did significantly correlate with several other behavioral sex-type measures. Given the inconsistent findings and paucity of relevant field research on boys' prenatal androgens and reproductive behaviors, more field research utilizing multiple lines of evidence will be helpful for interpreting the meaning and significance of these findings. For example, anogenital distance may be employed as a measure of prenatal androgen exposure, with researchers finding that boys' (masculinized) anogenital distances predicted more masculine/less feminine play behaviors at 3–4 years of age (Pasterski et al., 2015).

Further evidence suggests that post-natal gonadal activation ("mini puberty") has long-term effects organizing a broad range of adult male sexual phenotypes, such as hormone regulation and physical and behavioral development (Kuzawa et al., 2010; Lamminmäki et al., 2012). After birth, boys experience a surge of testosterone that reaches its peak around the third month before returning to prepubertal levels around the 6th–9th months (Kuzawa et al., 2010; Lamminmäki et al., 2012). Early postnatal testosterone levels have been reported to predict later male-typical psychosexual behaviors at age 14 months, as assessed with the PSAI, and preferred choice of play toys, such that testosterone correlated negatively in boys preference to play with baby dolls (Lamminmäki et al., 2012). In addition, Kuzawa et al. (2010) collected data from 770 Filipino men in their twenties and data on their weight velocities from birth to 6 months of age. They found that males who experienced faster postnatal growth were characterized by having higher levels of testosterone in adulthood, progressed through puberty sooner, were taller and more muscular, and reported having more lifetime sexual partners. These findings support the view that the postnatal period represents a critical developmental stage where testosterone release and growth trajectories orient life history strategies and male reproductive phenotypes.

Several researchers have speculated that a functional relationship exists between emergent sexual attraction and interest in the opposite sex and adrenal hormone production among juveniles (Ellis and Essex, 2007; Herdt and McClintock, 2000). The juvenile period begins around 6–8 years of age and coincides with the onset of adrenarche, the prepubertal increase in adrenal androgen secretion of DHEA and its metabolite androstenedione, androgens known to exert weak androgenic activity (Campbell, 2011; Mouritsen et al., 2013). This delayed reproductive maturity is hypothesized to be important for learning cultural, social, and ecological skills that help prepare the child for the adult reproductive socio-competitive environment (Del Giudice et al., 2015). Herdt and McClintock's (2000) analysis provides cross-cultural insight into the biological age in which boys begin to express sexual attraction toward others while giving considerations to potential organizational and activational effects of adrenal hormones in juvenile boys. They presented data from the Sambia in New Guinea and United States populations to reveal that in both societies boys develop, on average, a more adult-like understanding of sexuality and express sexual attraction toward others by the age of 10. The authors suggest that emergent sexual attraction and arousal is related to neuroendocrine changes associated with the onset of adrenarche. In support of this view, the authors note the role of DHEA as a primary sex hormone that can be converted to stronger sex-steroids (e.g., testosterone) and the association of adrenal hormones with adult sexual attraction and libido. However, direct field evidence of a link between juvenile male adrenal androgens and the development of sexual attraction is lacking.

DHEA and androstenedione have received little attention as important regulatory steroid hormones in the context of male-male competition in children or even adults. Recent evidence suggests that adrenal hormones may play an activational role in male-male competition during the juvenile period of development, a time in which adrenal gland activity is high and testosterone production is low (Campbell, 2006; Nelson, 2011). Two of the authors here (McHale and Gray) led the first published field study that simultaneously measured acute adrenal androgen (DHEA, androstenedione, and testosterone) and cortisol responses to physical competition in juvenile boy soccer players, 8 and 10 years of age, in Las Vegas, Nevada (McHale et al., 2016). Five teams of boys from the Downtown Las Vegas Soccer Club, an elite soccer franchise of highly competitive teams of athletes, provided saliva samples before and after a soccer practice ($N = 28$), with four out of five teams providing saliva samples before and after a soccer match ($N = 26$). The results indicate that salivary DHEA and androstenedione increased acutely in response to naturalistic intense forms of physical competition, while testosterone levels were below detection in almost all samples. Cortisol, a well-known biomarker for psychological and physical stress, did not significantly change during the soccer practice or match, possibly as a result of small sample size. The latter results conflict with those from another study which showed cortisol acutely

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increased in boys, 10 years of age ($N = 12$), in response to competing in a taekwondo competition (Capranica et al., 2012). Overall, McHale et al.'s (2016) preliminary findings raise the idea that juvenile boys may have evolved a functionally distinct endocrine pathway, implicating DHEA and androstenedione, that is activated in order to meet the physical and cognitive demands of male-male physical competition. Despite boys and girls experiencing a similar increase in circulating levels of adrenal hormone release during the juvenile period, cross-cultural behavioral data has identified that the juvenile period is characterized by heightened levels of play and the emergence and intensification of behavioral sex differences (e.g. Benenson et al., 2002; Geary et al., 2003). For example, on average, boys are more likely to engage in higher rates of rough-and-tumble play and spontaneously organize into large same-sex play groups, while girls exhibit a preference for play parenting and dyadic social relationships, mirroring sex-specific adult patterned behavior (e.g. Geary, 2010). One interpretation of these findings is that adrenarche may promote the emergence of behavioral sex differences that have already been organized perinatally in order to practice and prepare for the socio-competitive environments expected to be faced in adulthood. That said, it remains unclear whether boys' hypothalamic–pituitary–adrenal axis (HPA) responses are sensitive to physical and/or socio-competitive factors (e.g., winning/losing, individual performance) that have been observed to mediate hormonal responses to competition in the adult male literature (e.g., review in Oliveira and Oliveira, 2014). Given these novel findings, more field studies, across different cultural contexts, are warranted to determine the extent to which physical and non-physical bouts of male-male competition in boys, along with cognitive variables (e.g. winning/losing effects, team versus individual competition), potentially induce acute reactive changes in adrenal hormones.

While testosterone is considered the main androgenic hormone associated with aggressive behavior (Ramirez, 2003), the few studies on prepubescent boys' androgens and behavioral measures of aggression suggest that additional androgens warrant consideration. These latter studies employ baseline rather than reactive designs in testing for relationships between boys' hormone levels and measures of aggression. An observational study conducted on a classroom of 28 pre-school boys (mean age = 4.8 years) found a positive correlation between testosterone and aggression (Sánchez-Martın et al., 2000a, 2000b). A different study explored the relationship between social behaviors and DHEA, androstenedione, and testosterone in 5-year old Iberian boys ($N = 60$) (Azurmendi et al., 2006). Subjects' social interactions were videotaped daily during free play on the playground throughout a school year. The taped behaviors were used to evaluate the number of times participants engaged in three behavioral categories: aggression, non-aggressive dominance, and affiliation. Results revealed a positive correlation in the behavioral factor 'Provocation' (a type of aggression) and androstenedione. DHEA and testosterone were not correlated with any of the behavioral measures. Yet, clinical studies have reported associations between testosterone and DHEA levels with increased aggression in boys (see review Soma et al., 2015). Similarly, androstenedione was the only androgen measured to be positively correlated with 'acting out,' which was considered an attribute of aggression, in a study conducted on boys 10–14 years of age ($N = 56$) (Susman et al., 1987). Lastly, psychosocial variables, such as parenting styles and living with more directive mothers, have also been shown to moderate relationships between androstenedione, testosterone and aggressive behaviors in boys (Pascual-Sagastizabal et al., 2014; Sánchez-Martín et al., 2009). In sum, the findings here call attention to tentative links between boys' steroid hormones and aggression, while also highlighting a need for more attention to be given to life history stage (e.g., pre- or post-adrenarche), psychosocial factors such as motivation, and social context.

3.2. Field studies of adult human male hormones and physical competition

Competitive interactions rapidly increase testosterone concentrations in numerous species (see Wingfield et al., 1990; Oliveira, 2009; Carré and Olmstead, 2015 for review). The 'Challenge Hypothesis", originally developed to account for intra- and inter-species variation in testosterone concentrations in birds, indicates that testosterone fluctuates widely throughout the season and in response to social interactions. In monogamous male birds that provide paternal care, testosterone remains relatively low throughout the season and increases at the start of the breeding season as a means to initiate spermatogenesis, expression of secondary sex characteristics and the full display of male reproductive behavior. Testosterone further increases in response to intrasexual competitive interactions as a means to facilitate territorial and aggressive behavior. At the end of the mating season, testosterone returns to a constitutive baseline. Wingfield et al. (2001) proposed that the costs associated with maintaining elevated testosterone concentrations (e.g., decreased paternal care, increased risk for physical injury/death, depressed immune function, increased energetic demands) may have led to a highly flexible endocrine system capable of rapidly modulating testosterone in response to changes in the social environment. Although initially developed to account for hormone-behavior relationships in birds, evidence in support of the Challenge Hypothesis has been found in numerous species including fish (Oliveira, 2009), insects (Tibbetts and Huang, 2010), non-human primates (Muller and Wrangham, 2004), and humans (Archer, 2006).

In a series of experiments in non-human primates, Rose et al. (1972, 1975) found that male rhesus monkeys who won aggressive interactions experienced marked elevations in testosterone, while losers experienced decreased testosterone. These findings led Mazur (1976, 1985) to propose the Biosocial Model of Status whereby testosterone concentrations during competition will vary as a function of the outcome of the competitive interaction, with testosterone increasing with victory, and decreasing with defeat. Mazur (1976, 1985) hypothesized that divergent neuroendocrine responses in winners and losers may ultimately serve to modulate the organism's social behavior according to their current status. More specifically, a rise in testosterone after a victory may promote competitive/dominant behaviors aimed at defending/maintain one's social status. In contrast, a decrease in testosterone concentrations may promote submissive behaviors aimed at avoiding further threats to social status and/orphysical injury.

Athletic competition provides an ideal environment for studying hormone-behavior associations in humans. Similar to research in animal models, effects of competition outcome (win vs. loss), game venue (home vs. away), type of competition (individual vs. team competition) and anticipation of competition can be studied in the context of neuroendocrine function. In addition to such factors, researchers can also examine the extent to which subjective mood and perception of one's individual performance modulates neuroendocrine responses. Field research on nonhuman primates such as Old World monkeys and chimpanzees, ethnographic research on human hunter-gatherers, and experimental and observational psychological research on humans recognizes that distinctions between coalitionary membership (in/out groups) are quite common, readily activated, and sometimes flexible (e.g., Gat, 2006; Geary, 2010). Those observations offer support for drawing analogies between ancestral coalitionary competition and contemporary team sports competitions, even as other factors (e.g., timing, group sizes, immediate causes of competition) qualify that analogy.

Early support for the role of competition outcome in modulating testosterone concentrations came from work in male tennis players. Mazur and Lamb (1980) reported that winners of decisive matches had elevated testosterone concentrations post competition relative to losers. In contrast, no differences between winners and losers could be observed when the outcome of the match was close. Shortly after this study was published, Elias (1981) reported that male wrestlers who won a competition ($N = 7$) had elevated testosterone concentrations post-competition compared to male wrestlers who lost ($N = 6$). More recent studies involving team competitions (e.g., badminton, field hockey, soccer), which more closely approximates coalitional-type of competition, have yielded similar findings whereby winners of

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competition had relatively elevated testosterone concentrations relative to losers (Jiménez et al., 2012; Aguilar et al., 2013; Oliveira et al., 2009a, 2009b).

Notably, most of the research on testosterone responses to competitive interactions has been conducted in industrialized countries. However, more recent work with more traditional, non-industrialized cultures has emerged, and for the most part, results converge well with what has been found in industrialized cultures. For instance, one study investigated testosterone responses among a group of male Tsimane hunters living in lowland Bolivia ($N = 31$). Although not equivalent to athletic competitions such as tennis, soccer, or wrestling, the authors reported that males who killed an animal during the hunt had significantly higher testosterone concentrations relative to males who did not kill an animal (Trumble et al., 2013). The rise in testosterone after a successful kill may increase the reward value of hunting behavior, which may contribute to the persistence of hunting behavior in this population. Another study of male Tsimane forager-horticulturalists failed to find differences in testosterone reactivity patterns between winners and losers of soccer matches (Trumble et al., 2012). However, similar to research conducted in industrialized countries (Gonzalez-Bono et al., 1999; Edwards et al., 2006), the authors reported that those individuals (winners and losers) who reported relatively good individual performance demonstrated a more robust increase in testosterone concentrations compared to individuals reporting bad individual performance. Finally, in a relatively small study of men from a rural Dominican community, Flinn et al. (2012) examined testosterone reactivity patterns to victory and defeat during a dominos competition that was either played among members of the same village (in-group competition), or between members of different villages (out-group competition). Remarkably, winners had elevated testosterone concentrations relative to losers – but only when competing with members from the out-group (Flinn et al., 2012). It has been speculated that elevated testosterone concentrations may promote hostility/aggression toward the out-group, and at the same time promote cooperation/generosity toward the in-group (Diekhof et al., 2014). This hormonal mechanism driving in-group cooperation and out-group aggression would certainly be beneficial in the context of coalitional aggression. Consistent with this proposition, elevated testosterone concentrations are positively correlated with cooperative/generous behavior toward in-group members (Diekhof et al., 2014; Reimers and Diekhof, 2015) and with increased aggression toward out-group members (Reimers and Diekhof, 2015; but see Diekhof et al., 2014). Collectively, these findings suggest that testosterone concentrations respond rapidly to out-group competition, and that elevated testosterone concentrations may promote the expression in-group cooperation/generosity *and* out-group aggression/hostility.

Interestingly, other work suggests that direct participation in competition is not required for competition-induced changes in testosterone to occur. Specifically, male spectators watching their favorite soccer or basketball teams win a competition had elevated testosterone concentrations relative to spectators watching their favorite team lose (Bernhardt et al., 1998). Similarly, other research has found that male hockey players watching their team win a previous victory experience a robust increase in testosterone concentrations (40%) relative to watching a previous victory (Carré & Putnam, 2010). Collectively, these findings suggest that the vicarious experience of victory or defeat may produce testosterone reactivity patterns similar to those observed in athletes directly engaged in the competition.

The reciprocal component of Mazur (1976, 1985) suggests that changes in testosterone in response to competition will serve to modulate ongoing and/or future social behavior. Support for this hypothesis has been obtained in human laboratory studies whereby a rise in testosterone during competition positively predicts subsequent competitive motivation (Mehta and Josephs, 2006; Carré and McCormick, 2008), aggressive behavior (Carré et al., 2009; Carré et al., 2013, 2014), risk-taking (Apicella et al., 2014), and antagonistic behavior (Geniole et al., 2013). Similarly, research in animal models provides compelling support for the idea that competition-induced changes in testosterone modulate subsequent competitive and aggressive behavior (see Trainor et al., 2004; Gleason et al., 2009; Oliveira et al., 2009a, 2009b). For instance, male California mice that win an initial aggressive interaction are more aggressive in subsequent interactions, but only if they received an injection of testosterone after the victory (Trainor et al., 2004). Studies from athletic competition rarely examine effects of competition-induced testosterone responses on subsequent behavior. However, a recent study by Casto and Edwards (2015) with female soccer players found that changes in testosterone during competition were positively correlated with the extent to which women wanted to reconcile with their opponent – regardless of whether the outcome was a victory or defeat. These findings are consistent with a growing body of evidence indicating that despite testosterone's links to antisocial behavior, it may also be associated with prosocial behaviors within certain contexts (e.g., Boksem et al., 2013; Eisenegger et al., 2010).

With respect to human 'field' work, a number of studies have documented an anticipatory rise in testosterone prior to competition (Bateup et al., 2002; Booth et al., 1989; Mazur et al., 1997; Suay et al., 1999). To the extent that acute increases in testosterone promote competitive motivation and aggressive behavior (see Carré et al., 2011 and Carré and Olmstead, 2015 for reviews), it is reasonable to hypothesize that acute increases in testosterone prior to competition may influence athletic performance. In a study of 28 male judo fighters, Salvador et al. (1999) found that pre-competition testosterone concentrations were positively correlated with threat behavior (attack, fighting and threat). If such pre-competition testosterone concentrations represent an anticipatory rise in testosterone, the findings suggest that acutely elevated testosterone prior to competition may facilitate competitive and aggressive behavior. A recent study more directly tested this hypothesis in male hockey players. Comparing saliva samples from a resting baseline to those obtained prior to competition, Putnam and Carré (2012) found that location of the competition moderated the relationship between the pre-competition rise in testosterone and athletic performance. Specifically, a rise in testosterone prior to a game played in the opponents' venue (i.e., away game) was *negatively* correlated with performance, whereas a rise in testosterone prior to a game played in the team's home venue was positively (though not significantly) correlated with performance. These findings highlight the importance of considering game venue when studying hormone-behavior relationships in field studies. Finally, research with male rugby players found that individuals receiving positive feedback from their coaching staff prior to a competition demonstrated a rise in testosterone concentrations and performed better (Cook and Crewther, 2012).

In many sports, there is a clear home advantage effect whereby teams have a stronger record when playing in their home venue compared to their opponents' venue. Several arguments have been put forth to explain this home advantage effect including familiarity with the playing field/arena, referee biases toward the home team, stronger support from the home crowd, and less travel time for the home team (see Carron et al., 2005 for review). Some studies have provided circumstantial support for the idea that testosterone may in part contribute to the home advantage effect in sport. Neave and Wolfson (2003) studied male soccer players and reported that pre-game testosterone concentrations were higher prior to games played in the home venue compared to the opponents' venue. Similarly, Carré et al. (2006) found that male hockey players had elevated pre-game testosterone concentrations for home versus away games. Another study with male hockey players failed to find differences in pre-game testosterone concentrations, but did observe differences in testosterone responses to competition as a function of game location (Carré, 2009). In this study, the hockey team won a game at home and away against the same team (with a similar margin of victory). Results indicated that both victories yielded a significant increase in testosterone concentrations – yet the increase was much larger when the victory occurred in the team's home

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venue. A remarkably similar effect has been observed in California mice whereby a victory in a resident intruder paradigm promotes a robust increase in testosterone when it occurs in the animal's home cage, but not when it occurs in a neutral venue (Fuxjager et al., 2009).

3.3. Field studies of adult human male hormones and sexual behavior

Researchers have long been interested in the relationships between male testosterone and sexual behavior, with these interests yielding relevant insights from field studies too. Some studies have examined whether a man's baseline testosterone concentration (often assessed via a blood draw in a clinical facility) is associated with self-reported measures of his sexual behavior (e.g., Brown et al., 1978). Other studies have investigated the potential change in a man's testosterone level during different types of sexual behavior, such as masturbation or intercourse outside of a lab facility (e.g., Dabbs and Mohammed, 1992). Such studies recognize that hormones can both modify the likelihood of certain behaviors and be themselves altered by behaviors (i.e., the causal arrow points both directions, albeit in complex ways). Relatively few field studies have assessed hormones apart from testosterone, despite lab-based studies pointing to the relevance of oxytocin, vasopressin and prolactin (e.g., Kruger et al., 2003; Murphy et al., 1987). Moreover, a few studies suggest that males may exhibit changes in hormone levels in "courtship" encounters with potential mates, pointing to the relevance of male hormones, arousal and mating effort even preceding actual sexual behavior (e.g., Roney et al., 2003; van der Meij et al., 2008). Among 18 men in a rural village in the Caribbean island of Dominica, men's testosterone levels were higher after engaging in interactions with potential mates compared with interactions with female kin or the mates of male friends (Flinn et al., 2012).

In a study of Australian male skateboarders, young male skateboarders performed public tricks in front of either a male or attractive female viewer (Roney et al., 2010). Those skateboarders performing in front of the female viewer had higher salivary testosterone levels after the field experiment than those performing in front of the male viewer, with higher testosterone levels also positively related to taking more risks (aborting fewer tricks). This field study complements those several lab-based studies of young men's testosterone responses to courtship encounters with young women (e.g., Roney et al., 2007), including the roles of the androgen receptor and baseline cortisol in moderating the magnitude of reactive testosterone increases (Roney et al., 2010). Moreover, several lab studies suggest that exposure of men to female stimuli (e.g., perioovulatory vulvar odors (Cerda-Molina et al., 2013) and opposite-sex faces (Zilioli et al., 2014) can induce acute changes in men's testosterone. A small study of Argentinian tango dancers ($N = 11$ males) provided difficult-to-interpret findings suggestive of a possible elevation in men's testosterone initially when dancing with a partner to music, with that response attenuated by repeated dancing (Murcia et al., 2009).

A handful of field studies assess potential changes in men's testosterone to sexual behavior in non-lab settings. For partnered sexual activity at home, one of the first such studies incorporated only four heterosexual couples (Dabbs and Mohammed, 1992) but suggested elevated testosterone levels on nights involving sexual activity compared with non-sexual evenings. Other studies have been mixed (see review in Goldey and van Anders, 2015). In a field study at a Las Vegas sex club, changes in men's testosterone levels were assessed while either watching or engaging in sexual activity (Escasa et al., 2011). Results showed that men's testosterone levels increased overall, but that this increase was higher among those men engaging in sexual behavior compared to those watching sexual behavior. No age-related differences in the magnitude of men's testosterone responses were observed, however. This study suggests that not all sexual stimuli are created equal: different behaviors may entail differences in motivation and physical activity, underscoring the importance of social context. Further illustrating the importance of social context and life history to men's testosterone and sexual behavior, Gettler et al. (2013) found that recent fathers in Cebu City, Philippines experienced less of a baseline decrease in testosterone the more sexual behavior they reported with their partner.

Studies of men's testosterone and sexual behavior suggest either weak or null relationships, although other factors qualify these general observations. In a study of 11 couples, men's blood testosterone sampled regularly in a lab was not related to intercourse frequency across a span of three months (Persky et al., 1978). Among 33 young German men, blood testosterone levels sampled six times over a two-week span were positively associated with sexual experiences occurring around the days of sample collection (Knussmann et al., 1986). In a study of 119 young Australian male university students, men's testosterone was weakly but positively correlated with cumulative sexual experience (Peters et al., 2008). However, a different study of approximately 100 young American men found no relationship between men's recent sexual behavior and blood testosterone levels (Brown et al., 1978). In a study of Hadza hunter-gatherer and Datoga pastoralist androgen receptor polymorphisms and male reproductive success, shorter androgen receptor CAG repeats (indicative of greater "androgenicity") predicted more children, with this link mediated by self-reported aggression on a questionnaire (Butovskaya et al., 2015).

Relationships between baseline male testosterone and everyday sexual behavior may vary across the life course. In samples of young adult German and Austrian heterosexual males (but not homosexual Austrian males), lower 2D:4D (more masculinized) was positively related to lifetime number of sexual partners (Hönekopp et al., 2006). In a large panel study of U.S. adolescent males, monthly assessments of salivary testosterone were positively correlated with sexual activity (Halpern et al., 1998). In a large study of U.S. aging, involving more than 700 participants 57–85 years of age, men's reported lifetime number of sexual partners was positively related to their testosterone level, even after adjusting for a variety of potentially confounding variables such as medication use (Pollet et al., 2011). An earlier aging study of 220 men found that age-related declines in free testosterone partially mediated age-related decreases in partnered sexual behavior (Davidson et al., 1983). However, this was not found in a sample of 60 Israeli men 65–80 years of age (Sadowsky et al., 1993). Viewed across the life course, increases in male testosterone perinatally and during adolescence as well as decreases with advancing age may help foster adaptive life history allocations to sexual behavior (e.g., helping motivate sexual behavior in ways adaptive to enhancing lifetime reproductive success).

While lab studies have shown increases in hormones besides testosterone with human male sexual activity (e.g., Kruger et al., 2003), almost no such studies have been conducted in the field. Salivary oxytocin levels increased among young men after 10 min of self-stimulation at home, with oxytocin levels returning to baseline 40 min after the initiation of the behavior (de Jong et al., 2015). Among males participating in a lab setting, orgasm from intercourse was associated with much higher prolactin increases than masturbation-induced orgasm (Brody and Kruger, 2006). While some scholars (e.g., Brody and Kruger, 2006) suggest such increases in prolactin could dampen libido, perhaps also lowering testosterone, thus far only clinically-elevated prolactin (hyperprolactinemia) seems to consistently lower testosterone levels and male sexual desire and behavior (Grattan, 2015). Moreover, Gettler et al. (2012) reported positive correlations between non-fathers' recent and lifetime sexual activity and prolactin in the Philippines.

3.4. Field studies of human male hormones, partnering and paternal behavior

A sizable literature has addressed variation in human male testosterone levels with respect to partnership and paternal variables. Many of these studies fall under the umbrella of field studies, albeit with gray areas such as assessment of male family relationship parameters in

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clinical or psychology labs in some cases. One of us (Gray) lead-authored a 2009 review of this body of literature (Gray and Campbell, 2009), which we draw on here. We also feature publications since that time that further refine our understanding of field studies of human male testosterone, partnerships and paternal behavior.

As our 2009 review summarized, 10 of 11 North American studies showed that partnered men and/or fathers had lower testosterone levels than their single counterparts. Some moderators and mediators were also found within groups of family men, with partnership quality and measures of paternal care sometimes related to men's testosterone (e.g., Gray et al., 2002). Studies from outside North America revealed more varied associations between men's testosterone and family relationship status. While studies in Beijing, China (Gray et al., 2006), urban Jamaica (Gray et al., 2007a, 2007b), a rural village in Dominica (Gangestad et al., 2005) and among Hadza foragers in Tanzania (Muller et al., 2009) showed that fatherhood was associated with lower testosterone levels, this was not the case among urban Bangladeshi men (Chatterton et al., 2007) or among Datoga pastoralists in Tanzania (Muller et al., 2009). Some lessons from the review were that men's age (e.g, stronger associations were sometimes found in young adults), time of day (e.g., some associations were stronger in afternoon or evening samples than mornings), control variables (e.g., anthropometric measures of nutritional status such as waist-to-hip ratio, or WHR), and sociocultural context (e.g., contrast between null testosterone and extra pair sex in urban China vs. in a U.S. military sample) were potential contributors to men's testosterone and family relationships.

Table 1 presents what we view as some of the key studies along with their conceptual and empirical contributions to field studies of human male testosterone, partnering and paternal behavior. We include studies conducted since that 2009 review, but we also draw on previously published work discussed in that same 2009 review chapter if it helps illustrate an important element in the larger conceptual and empirical landscape. What are the take-home points of this evolving literature, including expanding number of field studies? One is that the details of male partnering and paternal care must be viewed within social context, an observation consistent with the recognition of considerable behavioral plasticity. For example, while fathers in rural Poland may engage in farming and other manual labor, that is less important in Zurich, even if fathers in both communities contribute by provisioning resources. Moreover, cross-cultural variation in human family arrangements provides an array of what can be viewed as natural experiments for investigating genetic bases and developmental and mechanistic plasticity in male social behavior. Rather than restrict analyses to Western, Educated, Industrialized, Rich and Democratic (WEIRD) societies (Henrich et al., 2010), these field studies include studies of men in polygynous marriages, same-sex unions, and involved in a variety of subsistence activities.

Another take-home point is that these studies are becoming more methodologically sophisticated. Several recent studies rely on samples of 100 s or even 1000s of men, in a few cases drawing upon representative samples. The incorporation of measures of individual differences (e.g., sensation-seeking) or other moderators (e.g., relationship quality) shows more nuance than earlier studies testing for testosterone differences by relationship or paternal status. Although not included in the Table, unpublished data from 100 Jamaican fathers of 18–24-month old children suggest partnership quality is higher among fathers with lower testosterone (Gray et al., in review). Several studies also sample the same subjects over time (e.g., in Zurich, Cebu City), which enables testing whether changes in men's family life lead to changes in men's testosterone levels. The longitudinal findings by Gettler et al. (2011a, 2011b) exemplify this important contribution by field studies on this topic.

Although outside the scope of the present review, additional lab-based studies have further clarified the processes connecting men's testosterone and family relationships. For example, brain imaging studies show the areas activated by exposure to child stimuli, helping clarify how hormone levels measured in peripheral samples may be involved in central effects (e.g., Feldman, 2015; Mascaro et al., 2013). Lab-based studies show that interacting with baby stimuli (e.g., dolls) can decrease men's testosterone if inducing a nurturant response, whereas men's testosterone may increase in response to the same stimuli if inducing a protective response (van Anders et al., 2014a, 2014b). Variation in fathers' testosterone responses to infant distress predicted paternal behaviors when those same children were one year of age (Kuo et al., 2016). However, other studies fail to observe short-term changes in fathers' testosterone during interactions with their children (e.g., Gettler et al., 2011a, 2011b), qualifying the naturalistic application of that distinction between nurturant and protective responses.

Besides the key findings (e.g., decreases in men's T after becoming fathers) already noted by Gettler and colleagues' research in Cebu City, Philippines, several other aspects of that research warrant attention here. The large and longitudinal design of this cohort study has enabled testing a variety of outcomes, including ones adding new insights into male hormones and reproductive behavior. While over 90% of fathers in the Cebu City sample co-slept with their young children, the exceptions—the non-co-sleeping fathers—had higher testosterone levels than their co-sleeping counterparts (Gettler et al., 2013). In considering the importance of paternal residence—whether or not a father lives with his child—residential fathers engaged in more hours of paid labor, childcare and fewer hours of recreation compared with non-residential fathers (Gettler et al., 2015). Paternal residence appears to play a small role in fathers' testosterone changes. However, in extending this work, analyses of approximately 300 blood spot prolactin levels among these fathers did not show any relationship to residence status (ibid.). The inclusion of prolactin represents another contribution of this body of work in Cebu City. The blood spots were obtained during home visits, and showed that fathers had higher prolactin levels than non-fathers (Gettler et al., 2012), with fathers of infants having marginally higher prolactin levels compared to fathers of older children (ibid.). Moreover, a sample of 42 Cebuano fathers of children also engaged in a standardized 30-min play session at home, providing blood spot samples from which prolactin levels were measured before and after the session. Fathers' prolactin levels decreased across the play session (Gettler et al., 2011a, 2011b). These prolactin findings show the important contrast between examining “baseline” and “reactive” hormone levels to a social variable, both of which can be meaningful. The finding of acute decreases in prolactin during a paternal interaction is difficult to interpret, with a few other studies (noted below) part of this complexity (see Grattan, 2015).

Besides work on testosterone, few field studies on hormones and human male partnerships and paternal behavior have been conducted. This is thus a general area where human findings lag considerably behind nonhuman animal models (e.g., experimental research on oxytocin, vasopressin and prolactin), in addition to a growing body of experimental human neuropeptide studies (see Bos et al., 2012). One lab-based study found that Canadian fathers displayed acute increases in prolactin levels to infant cries (Fleming et al., 2002). However, a different Canadian study found that fathers experienced decreases in prolactin levels during play with their toddlers (Storey et al., 2011), whereas a sample of Israeli fathers providing blood samples and engaging in standardized child play scenarios at home showed positive relationships between coordinated play and baseline prolactin levels (Gordon et al., 2010). It may be that fine-grained details of paternal motivation, paternal experience the same day prior to testing, and other factors contribute to the variable findings between fathers' prolactin and paternal responses (Storey et al., 2011).

There are empirical hints, some from field studies, that the oxytocin system may be involved in human male family life. In a study of 38 couples reporting to a lab, men with higher blood oxytocin levels were involved in more supportive relationships (Grewen et al., 2005). Men who had recently fallen in love within a romantic relationship had

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Table 1
Conceptually and empirically important testosterone and human male family relationships field studies.

Study population	Research design	Results and significance	Reference
U.S. Army veterans	4462 men (mean age = 37 years) providing one morning serum sample + demographic data during clinical visits	Married men had lower T; T was also positively associated with divorce and extramarital sex; first study to focus on men's T and family relationships	Booth and Dabbs (1993)
U.S. Air Force veterans	1881 men aged 32–68 providing morning serum samples 1–4 times over a 10-year time span + demographic data during clinical visits	Married men had lower T; men who divorced showed subsequent increases in T; first study to employ longitudinal assessment of men's T and relationship status changes	Mazur and Michalek (1998)
Canadian fathers	34 men provided blood samples around the time of their partner's birth	Fathers had lower T shortly after the birth of a child; first study to focus on T and fatherhood	Storey et al. (2000)
Boston-area men	58 men aged 21–40 providing morning and evening saliva samples + completing questionnaire	No morning differences in men's T by relationship status; married men had lower T; first study to consider both partnership and paternal behavior	Gray et al. (2002)
Kenyan Swahili	88 men aged 29–52 providing morning and evening saliva samples and demographic information in interviews	No differences in T levels between unmarried and monogamously married men, but men with two wives had higher T than other men; first study to consider polygynous marriage and T	Gray (2003)
Ariaal pastoralists, Kenya	203 men aged 20 and older provided morning and evening saliva samples and demographic information in interviews	Monogamously married men had lower T levels than unmarried men aged 20–39; no differences in T levels between monogamously and polygynously married men; included a wide age spread and samples along with related markers (e.g., androgen receptor polymorphisms)	Gray et al. (2007a, 2007b), Campbell et al. (2009)
Hadza foragers and Datoga pastoralists in Tanzania	31 Hadza men aged 17–72 and 85 Datoga men aged 18–68 providing morning and evening saliva samples and demographic information in interviews	T levels were lower among residential Hadza fathers, but did not differ by relationship status among Datoga men; cross-cultural comparison with a priori predictions related to patterns in men's T	Muller et al. (2009)
Senegal	81 men aged 18–70 provided 2 morning and 2 late afternoon saliva samples, with wives providing information on men's mating and parenting behaviors	Married fathers had lower T than unmarried non-fathers; among fathers, men providing more parental investment had lower T; interaction between men's age, marital status and testosterone: among men 50 years of age or younger, men with multiple wives had higher T, but polygynously married men older than 50 had lower T; important for cross-cultural scope among rural farmers and with measures of both mating and parenting effort	Alvergne et al. (2009)
Canadian samples	49 male university students provided 1 saliva sample and information on relationships; 127 male students from university and Pride Parade communities providing 1 saliva sample and demographic information	Partnered men had lower T than single men, whether these men were living in the same city or not as partners; Partnered men had lower T levels than singles if partnered with a woman but not with a man; these studies extended the scope of research to long-distance relationships and to include homosexual male participants, although subsequent findings on sexual orientation have differed	van Anders and Watson (2007), van Anders and Watson (2006)
Cebu City, Philippines	Approximately 600 community-dwelling young adult men in a cohort study provided 1 evening and 1 early morning saliva sample collected at home and participated in interviews and had anthropometrics taken	Men with higher initial testosterone (in 2005) were more likely to marry; among men, those who married and had a child had greater decreases in T than those who remained single; among fathers, those providing more care and with young infants had the lowest T; important for employing a longitudinal design to causally test the effect of fathering on men's T, and for drawing upon a rigorous and large study	Gettler et al. (2011a, 2011b)
Zurich, Switzerland fathers	75 men (37 fathers and 38 control non-fathers) provided saliva samples and completed scales, with fathers providing samples 4 weeks before and 8 weeks after a child's birth	Fathers had lower T than non-fathers; relationship quality decreased after childbirth, with tenderness in a relationship interacting with fatherhood to predict lower T; fathers with lower T also reported lower sensation seeking; important for testing interactions with other variables during family relationship transitions	Perini et al. (2012a, 2012b)
U.S. aging male sample	754 White U.S. males aged 57–85 as part of the National Social Life, Health and Aging Project (NSHAP) provided a saliva sample and answered questions about fertility and confounds	Childless males had higher T than men with children, but among fathers there was a positive relationship between T and number of children; important for focusing on older males and in a large, nationally representative sample	Pollet et al. (2013)
Cebu City, Philippines	Approximately 600 community-dwelling young adult men in a cohort study provided 1 evening and 1 early morning saliva sample collected at home and participated in interviews and had anthropometrics taken	Longitudinal changes in paternal care were linked to longitudinal changes in T: if fathers increased their caregiving their T went down over the 4.5-year follow up, whereas if fathers decreased their caregiving, their T went up.	Gettler et al. (2015)
Rural Poland	122 men aged 18–78 provided saliva samples, information on family life and anthropometrics and grip strength	T was lower among fathers than non-fathers, with fathers also showing more muscle mass and strength; notable for addressing T and provisioning among fathers in a society where many men are involved in manual labor	Alvarado et al. (2015)

higher blood oxytocin levels than singles (Schneiderman et al., 2012). The administration of intranasal oxytocin to men yielded relatively more positive couple interactions in a lab setting (Ditzen et al., 2009) and higher evaluations of the attractiveness of a beloved partner's face compared with control female faces (Scheele et al., 2013). Among a sample of men in Georgia involved in a hormone and brain imaging study, fathers had higher blood oxytocin levels than non-fathers (Mascaro et al., 2013), although no differences in urinary oxytocin were found between a sample of expectant Dutch fathers and non-fathers (Cohen-Bendahan et al., 2015) or among Jamaican fathers compared with non-fathers (Gray et al., 2007a, 2007b). Among a sample of 48 Israeli fathers of infants tested in a lab, blood oxytocin level was positively associated with affectionate contact during a brief interaction paradigm (Apter-Levi et al., 2014). In a study conducted at homes in Israel, 80 fathers had blood oxytocin measured and brief interactions with infants recorded and coded, showing that fathers' oxytocin level was positively associated with stimulatory play (Gordon et al., 2010). A few studies suggest involvement of oxytocin receptor polymorphisms

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in differential male family life (e.g., Schneiderman et al., 2014), although meta-analysis has yielded little support generally for a role of oxytocin receptor differences and human social behavior (Bakermans-Kranenburg and van IJzendoorn, 2014).

Despite the increased interest in oxytocin's links to human social behavior, a number of methodological concerns have been raised that also have relevance for human field studies. In a recent review of this literature, McCullough et al. (2013) found that many studies used unreliable assay methods that yield estimates of oxytocin that are much higher than earlier techniques using more validated but laborious extraction procedures. Other research used experimental manipulation of oxytocin through intranasal spray as a means to investigate the role of oxytocin in modulating human behavior. This approach achieved widespread popularity when Kosfeld et al. (2005) reported that a single 'sniff' of oxytocin increased trust. Unfortunately, this effect has not been replicated (Nave et al., 2015) and several authors have argued that the oxytocin administration literature is plagued by low powered studies (Walum et al., 2016), publication bias and false positives (Lane et al., 2016; Leng and Ludwig, 2016).

The effective lack of field research on human male vasopressin is remarkable, particularly in light of evidence from other taxa such as voles that the vasopressin system plays functional roles in male reproductive behavior (e.g., Carter, 2007; Donaldson and Young, 2008; Dumais and Veenema, 2016). Urinary vasopressin levels did not differ between partnered and single men in a sample of 45 Las Vegas males (Sanchez et al., 2009), nor between samples of fathers and non-fathers in Las Vegas (Steiner, 2011). No differences in urinary vasopressin were found between expectant fathers and non-fathers in a Dutch sample (Cohen-Bendahan et al., 2005) or among Jamaican fathers compared with non-fathers (Gray et al., 2007a, 2007b). However, Dutch fathers given intranasal vasopressin showed more interest in baby-related avatars in an artificial world (Cohen-Bendahan et al., 2005). In what could be defined as the only human male vasopressin and reproductive behavioral field study, polymorphisms in the vasopressin 1a receptor were associated with differences in partner bonding and likelihood of divorce in a Swedish sample (Walum et al., 2008). The functional significance of those polymorphisms is not clear, and the effect size small, even if the implication of the vasopressin system in male reproductive behavior is anticipated.

4. Part III. Critical evaluation and future directions

In reviewing the human male field studies of reproductive behavior, it is quite apparent that the field is patchy. Studies cluster around several topics at specific life stages: testosterone responses to young men's athletic competition, and variation in men's testosterone within family relationships during prime reproductive years. Few studies address male sexuality and competition among juveniles or in advancing ages. Despite theoretical and empirical impetus from nonhuman animal research, few field studies of male prolactin, oxytocin or vasopressin have been conducted. In the remainder of this section, we discuss key issues in conceptualizing and interpreting field studies of human male hormones and reproductive behavior while pointing to directions for future research.

The body of human male field studies of hormones and reproductive behavior raises key questions about research design. What behavioral phenotype will be assessed? How will it be measured? Some behaviors (such as wins or losses in an athletic competition) lend themselves more readily to straightforward measurement than others (e.g., assessment of a male's mate guarding behavior). Large, representative samples often employ cruder behavioral measures (e.g., interview assessments of relationship status conducted with many subjects) than smaller, more naturalistic studies. The deployment of a "baseline" vs. a "reactive" research design matters for behavioral assessment: interview, questionnaire or observational measures of paternal status and paternal investment may be linked with hormone measures in tests of association between variables, whereas paternal measures in an acute design may differ (e.g., how did the father behave during the specific time of focus)?

What hormone(s) will be measured, how often, when, and in what media (see Saxbe, 2008, for related discussion on human cortisol field studies)? While there is conceptual and empirical validity to contrasting "baseline" vs. "reactive" hormone-behavior paradigms (as in Gettler and colleagues' research in Cebu City, Philippines), the observation that experiences preceding collection of a "baseline" sample in a given day can impact that baseline level and response suggest how even this facet can be more complicated. Because different media have different time integrations (e.g., urine samples capturing longer durations of hormone release than, say, blood), this is one of several reasons for carefully considering one's choice of media and assay technique (e.g., Anestis, 2010). Also, time of day in which samples are collected may be an important factor to consider in future work. Some work suggests that links between testosterone ('baseline' and 'reactive') and social/behavioral processes may be stronger when the samples are collected in the afternoon relative to the morning (Muller et al., 2009; Roney et al., 2007). One potential reason for this effect is that testosterone concentrations are highly variable during the morning hours, introducing error variance and decreasing the likelihood of detecting hormone-behavior associations. Indeed, Kuzawa et al. (2016) have reported that testosterone concentrations undergo a sharp decline shortly after waking, such that more than 60% of the diurnal decline in testosterone occurs within the first 30 min of waking. Kuzawa et al. (2016) have speculated that testosterone may have different functions during sleep (reflected in samples collected immediately after waking) versus wake-cycle. Specifically, they argue that the relatively elevated testosterone concentrations observed overnight (during the sleep phase) may function to stimulate anabolic processes, such as the building and maintenance of skeletal muscles, whereas the lower testosterone levels during the day may be more closely linked to social/behavioral functions. In addition to time of day, other variables that need to be considered when designing field experiments in social endocrinology include subject age, anthropometrics, health status, and medication use (see van Anders et al., 2014a, 2014b).

What methodological considerations are important to human field research designs, including with respect to nonhuman field studies? While observational studies are the staple of nonhuman primate male field studies, many human behavioral phenotypes do not readily enable such measures (e.g., observation of human sexual behavior or physical aggression against a romantic partner). Long-term, longitudinal human field studies can provide rich individual and population-level insights but are rare, in part due to challenges of sustaining the necessary infrastructure and funding. These few such human field studies also tend to have small sample sizes. One benefit of human field studies, nonetheless, is the capacity for sampling larger number of subjects, including in particular social contexts (the sample sizes of human field studies regularly surpass those of nonhuman primates). Even then, however, the incorporation of control variables and the increasing desire to test for effects of specific moderators means that these human studies face important questions about effect size and statistical power.

There are many potentially fruitful future research avenues ahead. Theory and empirical evidence points to the importance of male paternity status and paternity certainty in structuring aspects of men's reproductive behavior (e.g., Daly and Wilson, 1998; Gray and Brown, 2015). However, no study has yet to test whether fathers' hormone responses to offspring care differ by these variables. For studies of coalitional aggression, scholars recognize the importance of in-group/out-group distinctions in cooperation vs. competition, including in chimpanzees (see Mitani et al., 2012). It has been proposed that oxytocin may enhance in-group biases in affiliative social behavior at expense to competing against out-group members (see Bartz et al., 2011; Trumble et al., 2015). However, a recent study found that Israeli Jewish adults given intranasal oxytocin showed increased empathy to pain of Palestinians,

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suggesting a wider cast to a possible social halo effect (Shamay-Tsoory et al., 2013). Several human studies suggest the importance of in/out group distinctions in male steroid hormone response (e.g., Flinn et al., 2012), though more could be done in this vein. Moreover, theory of male competition emphasizes competition against other males. But what happens when males compete against females? Does this attenuate male physiological responses to competition, or might it induce a show-off effect of increasing hormone response? In the only study, to our knowledge, that has addressed this issue, a field study of university male students competing in an ultimate Frisbee tournament displayed increased testosterone responses when competing against teams with relatively more females (Miller et al., 2012). Future research might also further explore naturalistic behavioral arenas such as men's hormone responses to sexual activity in brothels, or while playing violent video games, with the view that the salience of such behavioral contexts is instrumental to testing potential effects on hormone response.

Human male field studies show that men in energetically-constrained subsistence socioecologies (e.g., lower food availability, higher physical activity, more pathogen pressures) have lower chronic testosterone levels (e.g., Ache: Bribiescas, 2001; Ariaal: Gray et al., 2007a, 2007b; Tsimane: Trumble et al., 2012) than men in populations such as Boston, although this does not appear to hamper male hormone response to competition (Trumble et al., 2012). Research that investigates the role of chronic and acute health status could prove fruitful (see Shattuck and Muehlenbein, 2015) on male hormone responses to potential mates and competitors.

There have been few systematic field studies which explore the relationship between reproductive behaviors in boys and the role of organizational and activational adrenal hormone effects during childhood, especially juvenility. With the bulk of human male hormones and field research studies having focused on prime-aged adolescents and adults, much work could be done to investigate boys' and older adults' reproductive behavioral endocrinology to help cover the full life course. From a life history perspective, many questions remain unexplored regarding the functional role of adrenarche, including questions surrounding baseline and acute reactive effects, and how boys, who exhibit low concentrations of testosterone, mediate socially competitive challenges, such as physical and non-physical bouts of male-male competition. Future research might also advance by controlling for physical exertion by incorporating measures of heart rate monitoring during bouts of individual and coalitional team sports competitions. Furthermore, it remains to be seen whether boys will experience an acute rise in adrenal hormones during a non-physical competition, such as a video game or math competition, in order to meet the cognitive demands of specific socio-competitive environments. Exploring the development of HPA axis sensitivity to various socio-competitive cues in relevant cross-cultural contexts, such as outcome of contests, individual performance, in-group/out-group effects, factors which are known to influence adult male hormone response and behaviors, will provide novel insight into the proximate and ultimate roles of adrenal hormone response. Given the developmental timing in which juvenile boys begin to express sexual attraction, it is also conceivable that boys could also exhibit higher acute steroid hormone release performing an activity in front of girls in comparison to boys (see Roney et al., 2010).

Research on hormones and grandfathering warrants attention. Does caring for dependent-aged grandchild impact men's hormone profiles, in both chronic and acute contexts? Two recent studies conducted on large, representative samples of older men provide some related insight, but did not directly address this idea. The findings from Pollet et al. (2013) reported earlier and based on the NSHAP study of men aged 57–85 years showed that fathers had lower testosterone levels, and that men's fertility was positively related to testosterone. Gettler and Oka (2015) showed that in a different but representative and large U.S. sample that men with two sources of emotional support had lower testosterone levels. The same NSHAP study entailed measurement of urinary oxytocin and vasopressin among a large, representative sample of older men, enabling testing for associations between hormone levels and measures of men's reproductive behavior (see Reyes et al., 2014). We hope to have an answer in the near future whether invested grandfathers show increases oxytocin and vasopressin responses to interactions with grandchildren. Even with such possible work on grandfathering, it should be noted that very little research seeks to connect field studies of male hormones and reproductive behavior across the life course.

Research on human male vasopressin and reproductive behavior warrants focus. The nonhuman animal research on vasopressin and male social behavior provides an important phylogenetic, adaptive and mechanistic backdrop in which to conduct human field studies on male vasopressin and reproductive behavior (Adkins-Regan, 2005; Goodson and Thompson, 2010). The lack of studies on acute male vasopressin changes to male-male competitive challenges and little attention given to the role of the vasopressin system in men's partnering and paternal behaviors is notable. That said, there are also reasons to be cautious in how one designs, tests and interprets findings in this area. A recent study entailed giving men intranasal vasopressin to test for acute aggression responses in a lab setting, but yielded null findings, contrary to expectation (Brunnlieb et al., 2013). One of us (Gray) was particularly sobered in advising a Psychology PhD student whose dissertation research failed to induce increases in urinary vasopressin during lab exposure to erotic and infant audiovisual content (Steiner, 2011). There are likely many parallels to the burgeoning human oxytocin literature for human vasopressin research (e.g., Macdonald and Feifel, 2013): vasopressin levels measured in peripheral fluids may not be indicative of central vasopressin levels, particularly in specific brain structures, and any links between the hormone and behavior are subtle and contextual.

Research that expands the methodological and conceptual complexities of male hormones and social behavior is increasingly happening and offers further opportunity for future research. The dual hormone hypothesis (Mehta and Josephs, 2010) links testosterone and cortisol in a single model related to male competition, an example of a framework expanding beyond studies assessing one hormone and one behavior simultaneously. Specifically, a number of lab-based studies have now demonstrated that baseline testosterone concentrations are positively related to a number of processes relevant to mating effort, including dominance (Mehta and Josephs, 2010), aggression (Popma et al., 2007), and risk-taking (Mehta et al., 2015), but only among individual with relatively low baseline cortisol concentrations. Only a few field studies have directly tested the dual hormone hypothesis (Edwards and Casto, 2013; Sherman et al., 2015). In one study of high level executives, it was found that baseline testosterone concentrations were positively correlated with the number of subordinates over which the executives had authority, but only for those with relatively low baseline cortisol concentrations (Sherman et al., 2015). The well-recognized links between male androgens and the vasopressin system (e.g., Dumais and Veenema, 2016) helps make an empirical basis for studies that synergistically link those two hormones in studies. In that vein, an instructive contrast between the views in van Anders et al. (2011) and Goodson (2012) helps show how such work might be conceptualized in future human male field studies as well as some of the challenges of doing this kind of human research.

Studies that link the endocrine system with other physiological systems (e.g., immune system, microbiome) can be situated within life history frameworks (e.g., organisms trading off survival vs. reproduction), development, and mechanism (how does the microbiome impact hormonal responses to potential mates, for example?). Moreover, a few studies cited in the present review include hormone receptor polymorphisms (e.g., Walum et al., 2008). Those studies are instructive in illuminating the small effect sizes, but the attention to receptor genes as well as receptor neural localization helps refine an understanding of physiological action of hormones as well as individual differences in response. While human intranasal oxytocin studies have exploded rapidly in

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number, motivated in part by potential therapeutic benefits, it is notable that these intranasal studies generally lack field measures of behavior (see Bos et al., 2012). The growing inclusion of experimental testosterone manipulations (e.g., Goetz et al., 2014; Carré et al., 2015; Welling et al., 2016) could also better quantify effects in naturalistic male social behavior such as athletic competition. Even then, however, the type and delivery of hormone (e.g., acute suppression of men's testosterone with GnRH antagonist) and typically 1-time hormone administration do not necessarily replicate endogenous production and action, even though such experimental interventions enable causal insight of hormones on naturalistic human social behavior.

Although winning is typically associated with elevated testosterone concentrations relative to losing (see Archer, 2006 for meta-analysis), there is quite a lot of variability in the extent to which this effect is found. We suspect that there are moderator variables that may influence the degree to which the winner/loser effect is found. For instance, in lab-based competition studies, Schultheiss et al. (2005) have found that winners have elevated testosterone concentrations relative to losers, but only to the extent that they score high on a measure of implicit dominance motivation. More recently, one of us (Carré) has found that individual differences in the extent to which one considers the self as independent vs. interdependent of other (i.e., self-construal) moderates the effect of competition outcome on testosterone secretion (Welker et al., under review). Specifically, winners have elevated testosterone concentrations relative to losers, but only for individuals with relatively independent self-construals (which is more typical of Western cultures). Thus, in addition to contextual factors such as where the competition was played (home vs. away; Carré, 2009) and against who the competition was played (ingroup vs. outgroup; Flinn et al., 2012), individual differences in personality traits may exert important moderating effects on testosterone reactivity to competitive interactions. In concluding with that observation, we underscore how human male field studies of hormones and reproductive behavior reviewed here have already made considerable theoretical and empirical impact, but also offer exciting prospects ahead.

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