# Chapter 22 The Neurobiology of Human Social Behavior: A Review of How Testosterone and Cortisol Underpin Competition and Affiliation Dynamics



#### Joey T. Cheng and Olga Kornienko

Abstract The brain, behavior, and neuroendocrine system have coevolved to support human group living. Recent developments in behavioral endocrinology over last several decades increasingly point to the powerful role of social experiences in influencing and being influenced by hormones. Here, we review the accumulated empirical developments that link two hormones-testosterone and cortisol-to social competition and affiliation. We suggest that testosterone and cortisol both influence and reflect the dynamics of human social behavior in domains of competition and affiliation, albeit in very different ways. The evidence supports the notion that testosterone may function as a competition hormone that calibrates psychological systems to current social standing and adaptively guide status-seeking efforts. As for cortisol, much evidence reveals that cortisol modulates affiliative behaviors in ways that appear to be adaptive; cortisol is elevated during times of social threat, social isolation, and loneliness, possibly to mobilize responses geared toward seeking coping and support, but is dampened when individuals gain social control and affiliative support. Still, more work is needed to unpack the complex interplay between neurobiology and human sociality. We end with a number of methodological recommendations on how using salivary bioscience methods may ultimately lead to a richer understanding of the complex reciprocal ties between biology and human social behavior.

 $\textbf{Keywords} \hspace{0.1in} \text{Testosterone} \cdot \text{Cortisol} \cdot \text{Competition} \cdot \text{Affiliation} \cdot \text{Social status} \cdot \text{Stress}$ 

J. T. Cheng (🖂)

O. Kornienko Department of Psychology, George Mason University, Fairfax, VA, USA e-mail: okornien@gmu.edu

© Springer Nature Switzerland AG 2020

D. A. Granger, M. K. Taylor (eds.), *Salivary Bioscience*, https://doi.org/10.1007/978-3-030-35784-9\_22

519

Department of Psychology, York University, Toronto, ON, Canada e-mail: chengjt@yorku.ca

# 22.1 History of Salivary Bioscience in Social Competition and Affiliation Dynamics

The study of hormones and social behavior in primates using salivary methods, which began a little over two decades ago, has since become an indispensable tool kit for understanding the interplay between neuroendocrinology and the social faculties of diverse species. Most notably, this work has made substantial contributions to our understanding of the social correlates of stress and the role of androgens in competition. In the earliest studies, salivary cortisol was sampled to study the effects of social interactions on stress in infant rhesus monkeys (Boyce, Champoux, Suomi, & Gunnar, 1995), and then later in squirrel monkeys (Fuchs, Kirschbaum, Benisch, & Bieser, 1997), tree shrews (Ohl, Kirschbaum, & Fuchs, 1999), adult rhesus monkeys (Lutz, Tiefenbacher, Jorgensen, Meyer, & Novak, 2000), and humans (Davis & Emory, 1995). In contrast, the application of salivary testosterone to studying primate social behavior, most notably aggression and competitive behavior, is comparably more recent, despite early validation work undertaken with rhesus monkeys (Arslan, Akhtar, & Nieschlag, 1984), and is more widely adopted in studies of humans than other primates (Dabbs, 1993), for which measures from urinary and fecal samples are widely used (Anestis, 2006; Beehner, Bergman, Cheney, Seyfarth, & Whitten, 2006; Behringer, Deschner, Deimel, Stevens, & Hohmann, 2014; Kutsukake et al., 2009).

The popularity of salivary cortisol and testosterone is driven by the many advantages they present over other methods. For example, approaches that rely on blood plasma sampling often require capture, restraint, and perhaps even sedation, thus inducing substantial stress. Moreover, the collection of urine, feces, or hair is often limited by availability, making difficult repeated sampling within short spans of time, such as in investigations of hormone reactivity or diurnal rhythm. On the contrary, salivary cortisol and testosterone are relatively easy to collect and store, and can be assessed repeatedly insofar as subjects can be trained to suck or chew on an absorbent material. Compared to their alternatives, salivary methods are less invasive and stress-inducing (though in nonhuman primates restraint is still sometimes required), and provide temporally sensitive measurements within a short intersampling interval (Behringer & Deschner, 2017; Kutsukake et al., 2009; Novak, Hamel, Kelly, Dettmer, & Meyer, 2013).

### 22.2 Current Status of Knowledge in Testosterone and Human Social Competition

We begin this review by surveying the extant evidence on the steroid hormone testosterone as a proximate mediator of human competitive social behavior. We propose that this evidence is best viewed in light of theorizing that emphasizes how testosterone (T), a principal androgen regulated by the hypothalamic–pituitary–

gonadal (HPG) axis, functions as a "competition hormone," readying individuals for and facilitating the attainment of social status. In constructing this empirical review, we rely on large assemblies of empirical studies, and, when available, meta-analyses to identify central areas of insight stemming from studies on T. Using this approach, we identified five key insights into T and competitive social behavior in humans:

- Does T cause aggression? A straightforward, one-to-one association between T and aggression is unlikely.
- Nevertheless, there is mounting evidence that T underpins a range of competitive motivation, behaviors, strategies, and propensities in humans.
- · Conversely, T also responds to social contexts and experiences.
- T rises during the anticipation of competition, in order to prepare the organism for challenge.
- T responds to competitive outcomes, rising following victory and falling following defeat.

#### 22.2.1 Is Testosterone a Causal Agent of Aggression?

Converging lines of animal research appear to suggest that aggressive behavior across diverse nonhuman species is, in part, facilitated by T. The earliest evidence for the inductive effect of T on aggression comes, for instance, from studies of rodents and red deer stags that reveal how individuals whose circulating T is suppressed or removed by castration show an absence of agonistic behavior; however, after T is supplemented and restored, fighting resumes (Beeman, 1947; Lincoln, Guinness, & Short, 1972). Conversely, aggression also influences T levels. This regularity is captured by the now well-supported challenge hypothesis (Wingfield, 2017; Wingfield, Hegner, Dufty, & Ball, 1990; Wingfield et al., 2000), which proposes that T fluctuates in concert with challenges-rising during the mating season when aggression is most intense in sexual competition for mates, but falling when physical contests are infrequent (e.g., during non-mating season or periods marked by paternal care or social stability). Consistent with this, early evidence in male birds point to seasonal variation in aggression coinciding robustly with seasonal variation in T, with a high peak of T during the height of intrasexual aggressive competition for females (Beletsky, Orians, & Wingfield, 1992; Vleck & Brown, 1999). Though the challenge hypothesis was initially conceived to explain patterns of androgenic activity birds, the last decades have seen substantial evidence confirming the key predictions that stem from this theorizing in diverse species (Archer, 2006; Hirschenhauser & Oliveira, 2006). However, it must be noted that substantial variation exists both within- and across-species and these effects appear to depend substantially on social context and environmental influences, many of which are still largely unknown (Wingfield, Ball, Dufty, Hegner, & Ramenofsky, 1987).

Does this link between T and aggression in nonhuman animals generalize to humans? The prevailing consensus is yes, but with a caveat: The link is weak at best

(Archer, 2006). Over the years, a series of meta-analyses of the numerous studies have been performed; all converge on the conclusion that the link between T and aggression in humans is weak but positive (in the range of r = 0.08 to 0.14), but is also inconsistent and highly variable (Archer, Graham-Kevan, & Davies, 2005; Book, Starzyk, & Quinsey, 2001). What explains the observed empirical inconsistency that plagues this literature? A key issue may be that aggression in humans is complex and non-unidimensional (Brain & Haug, 1992; Carré & Olmstead, 2015; Wrangham, 2018). While some forms of aggression are direct and physical (the variety studied in other mammals), others are indirect and nonphysical (Archer, 2004; Archer & Coyne, 2005). The clearest evidence on physical aggression comes from a large-scale study showing that male prisoners with higher salivary T are more likely to have a history of violent crime (such as homicide, assault, robbery, and rape), but less likely to have a record involving nonviolent crimes (such as theft and drugs; Dabbs, Carr, Frady, & Riad, 1995, Dabbs, Frady, Carr, & Besch, 1987). Similar patterns are found in female prison inmates (Dabbs & Hargrove, 1997). Nevertheless, evidence on physical aggression (and its relations to T) remains limited still. After all, human physical aggression is relatively rare (compared to other species) and conflict is often resolved without escalation (Cant, English, Reeve, & Field, 2006), both of which restrict opportunities for research.

In part out of necessity then, the bulk of other available evidence addressing T and aggression in human relies on indirect aggression or aggressive motivation, rather than threat postures and actual fights (as in studies of nonhuman animals). But even so, the evidence based on these measures still appears mixed. Stronger positive associations are sometimes obtained in studies using peer reports (in contrast to selfreports) of aggressive intent or hostility (Archer, 1991; Assari, Caldwell, & Zimmerman, 2014; Persky, Smith, & Basu, 1971), and salivary T compared to other sampling methods (Archer, Birring, & Wu, 1998). Meanwhile, laboratorybased studies that attempt to simulate and capture actual aggressive behavior (such as using willingness to inflict harm by blasting an opponent with aversive sound) have similarly produced mixed results, reporting positive, null, or sometimes even negative associations with salivary T (Buades-Rotger et al., 2016; Carré, McCormick, & Hariri, 2011). Perhaps most problematically, a causal effect of T cannot be confirmed given emerging null evidence of T induction in these laboratory situations (Boksem et al., 2013; Eisenegger, Naef, Snozzi, Heinrichs, & Fehr, 2010; Zethraeus et al., 2009). Overall, given these conceptual and methodological differences, it is unsurprising that studies often yield different estimates of the link between T and aggressiveness. Another issue is that existing studies of T are bedeviled by small samples that hinder the search for firm conclusions (Geniole, Bird, Ruddick, & Carré, 2017). In summary, though the evidence is plentiful, the results are mixed and indicate, at best, a weak positive link between T and aggression in humans (Carré & Olmstead, 2015).<sup>1</sup>

<sup>&</sup>lt;sup>1</sup>Note that although steroid hormones have long been a focus in the study of aggression, it is important to keep in mind that aggressive behavior is ultimately determined by complex interactions

#### 22.2.2 Testosterone Underpins Human Competitive Behavior

In light of this controversial, and at best minor, influence of T on human aggression, where does this leave our understanding of the role of T in social behavior? In recent years, an emerging new perspective is that T functions as a "competition hormone" that readies and calibrates an organism's psychology for the pursuit and maintenance of status and by doing so maximizes fitness across competitive contexts (Booth, Granger, Mazur, & Kivlighan, 2006; Eisenegger, Haushofer, & Fehr, 2011; Knight & Mehta, 2014; Mazur & Booth, 1998). In contrast to the early (and perhaps overly simplistic) claim of a one-to-one link between T and human aggression, this revised notion emphasizes the role of T in activating a suite of competitive motivation, behaviors, and strategies that altogether coordinate a complex, integrated behavioral repertoire that facilitates the pursuit and maintenance of status. Unlike the case for aggression, this newly emerging integrated and nuanced view is finding broad and robust support in diverse empirical research programs. In the remainder of this section, we provide a brief review of the relevant evidence, which can be parsed into three interconnected literatures: (a) the effects of T on status-enhancing motivation and behaviors; (b) an anticipatory T increase before an impending competition; and (c) the modulation of T by the outcome of competitions (success and defeat).

#### 22.2.2.1 Testosterone Propels Interlocking Motivation, Behaviors, and Strategies that Enhance Social Status

Diverse lines of research are converging on the notion that T facilitates status attainment in humans by propelling a repertoire of competitive psychology and behavior. First, evincing the key role of T in status-seeking efforts, endogenous T (or, baseline levels of T)—which in many existing studies are assessed using a single saliva sample—are positively correlated with a range of cognitive states and behaviors that increase the success and competitiveness of an individual in competitive situations and conflict. This collection of cognitive states includes those that directly and indirectly increase one's odds of prevailing in conflict—such as implicit power motivation (Schultheiss, Wirth, & Stanton, 2004; Schultheiss et al., 2005; Stanton & Schultheiss, 2009), risk-taking in economic domains (Apicella, Carré, & Dreber, 2015; Apicella et al., 2008; Coates, Gurnell, & Sarnyai, 2010; Sapienza, Zingales, & Maestripieri, 2009), overconfidence (Johnson et al., 2006; Ronay, Tybur, van Huijstee, & Morssinkhof, 2017), intuitive (rather than deliberate) and "hawkish" decision-making (Mehta, Lawless DesJardins, van Vugt, & Josephs, 2017; Nave,

between genes (e.g., MAOA genotype), biological signals (e.g., dopamine receptors, steroid hormones including T and estrogen), neural circuits (e.g., amygdala, frontal cortex suppression), and gene-environmental interactions. Hormones do not function in isolation (Batrinos, 2012; Nelson & Trainor, 2007).

Nadler, Zava, & Camerer, 2017), persistence (Andrew & Rogers, 1972; Archer, 1977), willingness to enter competitive interactions (Carré & McCormick, 2008; Coates, Gurnell, & Rustichini, 2009; Mehta & Josephs, 2006), and reduced sensitivity to threat (Hermans et al., 2007; Hermans, Putman, Baas, Koppeschaar, & Honk, 2006; van Honk & Schutter, 2007; van Honk et al., 1999). Behaviorally, higher T is associated with conspicuous consumption to increase perceived status (Nave et al., 2018; Wu, Eisenegger, Sivanathan, Crockett, & Clark, 2017), calling the bluffs of opponents (van Honk et al., 2016), and making more threats, confrontations, and rule infractions in prison (Dabbs et al., 1995; Dabbs & Hargrove, 1997).

Of these results, the effects of T in increasing concern for status and reputation are particularly well illustrated by three sets of laboratory findings. First, Josephs, Sellers, Newman, and Mehta (2006) assigned individuals to high- or low-status treatments to compare how the physiological, emotional, and cognitive states elicited might differ across people with different levels of T. Their results reveal that placing high T individuals in a low-status position created much distress, including inducing negative affect and physiological arousal, heightening their mental preoccupation with status cues, and suppressing their cognitive functioning and performance. Second, building on this evidence, Mehta, Jones, and Josephs (2008) further demonstrated that the consequences of low status vary across men with different levels of T. They found that cortisol rises sharply among high T men following a loss of status (defeat in a competition) but drops in high T men who gain status by winning. Highlighting the role of T in status concerns, in low T men, no changes in cortisol were observed after victory or defeat. Third, further illustrating the link between T and status-seeking, more recent behavioral evidence shows that high T individuals show more characteristic dominant ethological displays, including selfish and forceful gestures and verbal statements, and disproportionate claims to shared resources (Mehta et al., 2017; Slatcher, Mehta, & Josephs, 2011). In sum, there is strong and abundant empirical support for the notion that androgen levels predict a wellcoordinated repertoire of motivations and behaviors that regulate and increase one's status and influence.

# 22.2.2.2 The Modulation of Testosterone by Context: Competition and the Outcome of Conflicts (Winning and Losing)

Above, we have seen how T is a potent proximate mechanism that contributes to regulating competitive behavior. However, T not only propels behavior but also responds to them, meaning that the social environment, in turn, also affects T levels (Mazur & Booth, 1998; van Anders & Watson, 2006). Since its inception over half a century ago, a long-standing interest in the field of behavioral endocrinology entails establishing precisely how endocrine systems interact with social stimuli to jointly regulate the expression of behavior (Beach, 1948; Ford & Beach, 1951). While earlier work has tended to focus on the response of the hypothalamic-pituitary-adrenal (HPA) axis to stressors (Kudielka & Kirschbaum, 2005; Tsigos & Chrousos, 2002), only more recently has research turned to exploring how the HPG responds to

social environments. Before proceeding, let us consider why, theoretically, T might be expected to vary in response to social situations.

Despite the advantages of high T in enhancing success in competitions (and hence success in mating, territorial defense, resource acquisition, and so forth), prolonged T elevation presents substantial costs, including high energetic demands, depressed immune function, increased risk of parasitic infestation and mortality, and suppressed investment in the care of offspring (Folstad & Karter, 1992; Lynn, 2016; Oliveira, 2004; Wingfield, Lynn, & Soma, 2001). As a result, males in many species face a trade-off between competitive inclinations (due to its facilitation of mating effort) and parental effort. Possibly owing to this trade-off, rather than remain persistently elevated, in many species T levels respond flexibly to context (Harding, 1981). The challenge hypothesis predicts long-term (seasonal) and shortterm patterns of T modulation that correlate with mating and parenting efforts (Wingfield et al., 1990). This means that T should rise in response to challenges when increased competitiveness is particularly advantageous, but dampen during periods when care of offspring is paramount. In this section, we review two major lines of empirical evidence supporting these context effects on T, and (given our particular interest here on competitive behavior) with a focus on work showing that T responds to situations involving (a) social challenge, such as in male-male competition; and (b) social victory and defeat.<sup>2</sup>

#### Testosterone Responds to Competition and Social Challenges

One of the most compelling lines of evidence for context effects is that, across diverse species, androgens are modulated by competition. If, as discussed above, T responsiveness is favored by intrasexual selection to turn on or off androgendependent behaviors to facilitate mating efforts, a similar T response should also

 $<sup>^{2}</sup>$ One of the first published reports documenting an effect of T modulation by social experience appeared in somewhat unusual circumstances. In 1970, an anonymous author published a report in the journal Nature (Anonymous, 1970). This communication, entitled "Effects of sexual activity on beard growth in men," reports the author's study of his own personal experience. Having lived in isolation on a remote island for two years, the author noticed what appeared to be a correlation between his beard growth and the timing of visit to the mainland where his fiancée resided. He noticed that when in isolation, his beard grew slowly, but just before his visit to the mainland, it would grow quickly. Inspired by this initial observation, he carried out a detailed study, meticulously quantifying his beard growth by collecting and weighing his beard shavings daily. Confirming his hunch, the data reveal a progressive increase in beard growth in the days that led up to his visit. In fact, he noticed that the longer the period of abstinence, the more obvious the anticipatory response. He concluded that the mere expectation of sexual activity served as a stimulus for his accelerated beard growth. He surmised that beard growth acts as a proxy for androgenic activity, and that the anticipation of sexual activity triggers androgen production, in turn stimulating beard growth. As we summarize in this chapter, subsequent research, some of which might well have been inspired by this anonymous author's experimentation, reveals qualitatively similar patterns that point to the role of sexual activity and its anticipation in inducing T production in men.

emerge in a range of situations involving competition with other males, given that male-male conflicts represent a primary means through which males compete, both directly and indirectly, for access to females. Evolutionary logic proposes that T responses to competition should operate in two principle ways (Archer, 2006; Mazur & Booth, 1998): (a) T should rise in anticipation of competition to prepare the organism for impending contest; and (b) following the competition, T should be elevated in winners but suppressed in losers to adaptively modulate future competitive motivation. We discuss these two ways in which T responds to competition next.

#### Testosterone Rises in Anticipation of Competition

An anticipatory androgen responsiveness to competition allows an individual to better adjust and regulate its subsequent behavioral output to the current context. That is, given the physiological effects of androgens on competitive ability, ranging from muscular development to rapid dampening of anxiety responses (Aikey, Nyby, Anmuth, & James, 2002; Celec, Ostatníková, & Hodosy, 2015), an anticipatory androgen response to contest may facilitate subsequent competitive behavior expressed in territorial defense, mate-guarding, and status contests (Carré & Olmstead, 2015).

Indeed, numerous studies performed on a range of species confirm an anticipatory T effect. These studies show that challenges from conspecific males in competitive encounters lead to a spike in T production in males, including primates (Cavigelli & Pereira, 2000; Harding, 1981; Loren Buck & Barnes, 2003; Muller & Wrangham, 2004; Rose, Holaday, & Bernstein, 1971). Interestingly, this effect may even operate on bystanders uninvolved in the fight but in whom aggressive motivation is merely primed (Clotfelter & Paolino, 2003; Oliveira, Lopes, Carneiro, & Canário, 2001). In the case of humans, similar evidence of an anticipatory T effect is observed in studies that track endocrine activity in the moments that precede the competition, many of which in the form of competitive sports and contrived laboratory competitions that attempt to simulate real-life human dominance contests. In their now classic tennis study, Booth, Shelley, Mazur, Tharp, and Kittok (1989) found that players displayed an anticipatory rise of T, as evidenced in their higher salivary T measured 15 min before the match compared to a baseline T assessed the day prior. Similar patterns of T rise before the competitive encounter have been observed in judo, wrestling, hockey, chess, and video game tournaments (Booth, Mazur, & Dabbs, 1993; Mazur, Booth, & Dabbs, 1992; Mazur, Susman, & Edelbrock, 1997; Salvador, Suay, González-Bono, & Serrano, 2003; Salvador, Suay, Martinez-Sanchis, Simon, & Brain, 1999), though note that the use of small samples remains as a key limitation of many of these studies.

# *Testosterone Responds to Contest Outcomes: Rising After Success and Falling After Defeat*

Beyond an anticipatory T response, another hormonal adaptation that may enhance success in competitive interactions is a flexible T response that takes into account the current competitive standing of the self vis-à-vis the rival, foremost in the form of a T rise during victory and T decline during defeat. This highly specific pattern of T response may act as an adaptive mechanism to adjust future behavior, such that future competitive behavior is facilitated in winners to prepare for future challenges, but dampened in losers whose withdrawal from future challenges minimizes costs from further injury and loss in status (Carré et al., 2011; Carré & Olmstead, 2015; Mazur & Booth, 1998; Mehta & Josephs, 2006; Zilioli & Bird, 2017). These outcome-dependent T changes may thus be functionally similar to other statusdependent changes in morphology (e.g., alterations in facial coloration and other sexual adornments, testicular size) and behavior (e.g., sociality) that occur when adult males rise or fall in social contests. That is, these changes may be considered part of a broader suite of behavioral and physiological adaptations for calibrating ongoing and future behavior in intrasexual competition (Setchell & Dixson, 2001; Wingfield et al., 1990).

Evidence indicates that a wide range of social mammals calibrate their T levels to wins and losses (Mazur & Booth, 1998). Winners of status contests generally show a rapid increase in circulating T relative to pre-competition or losers in physically demanding competitions, such as wrestling, rowing, and tennis (Booth et al., 1989; Elias, 1981; Longman, Surbey, Stock, & Wells, 2018; Mazur & Lamb, 1980), as well as nonphysical competitions with sanctioned competitors, such as chess, domino, and video game matches (Flinn, Ponzi, & Muehlenbein, 2012; Mazur et al., 1992; Zilioli & Watson, 2012). This victory-induced T effect is particularly pronounced when the stakes of competition (and thus competitive motivation) are especially high, such as when status concerns are hyper-salient and the domain of competition has high self-importance (Edwards, Wetzel, & Wyner, 2006; Schultheiss et al., 2005; Vongas & Al Hajj, 2017), the competition venue is in own territory rather than away (i.e., "home advantage;" Carré, 2009; Fuxjager, Mast, Becker, & Marler, 2009; Neave & Wolfson, 2003), or the defeated rival is from an antagonistic out-group rather than in-group (Flinn et al., 2012; Oxford, Ponzi, & Geary, 2010).

A key issue in these earlier studies on victory-induced T effects, however, is that causality cannot be firmly established. A rising T profile may be a cause (rather than a consequence) of winning, thus leaving the possibility of reciprocal causality on the table. Recent laboratory experiments, however, have dramatically clarified the causal basis. Using rigged competitions to manipulate wins versus losses, a number of studies confirm a causal effect of winning on elevated T (Gladue, Boechler, & McCaul, 1989; Josephs, Newman, Brown, & Beer, 2003; Josephs et al., 2006; Longman et al., 2018; Newman, Sellers, & Josephs, 2005; Schultheiss et al., 2005; Zilioli & Watson, 2012, 2014; but see Wu et al., 2017). These results are obtained even when the outcome is knowingly chance-based and independent of ability (e.g.,

coin-tosses; McCaul, Gladue, & Joppa, 1992), and victory is experiential rather than personal, such as for fans of a winning soccer team and supporters of a winning political candidate (Bernhardt, Dabbs, Fielden, & Lutter, 1998; Stanton, Beehner, Saini, Kuhn, & LaBar, 2009). This causal effect of winning on T can be sizable; for example, a 40% T increase is induced by simply watching one's previous victory on video (Carré & Putnam, 2010). Taken together, these lines of evidence from a range of competitive contexts indicate that winners display a greater rise in T than losers, supporting the notion that these context-dependent T responses provide organisms with feedback on prior social experiences to effectively calibrate future competitive efforts.

In summary, converging lines of evidence indicate that T predicts as well as responds to competitive interactions; it is both a cause and a consequence of social challenge.

#### *Testosterone Facilitates the Competition for Social Status Based on Both Dominance (Agonistic Contests Based on Fear) and Prestige (Non-agonistic Contests Based on Respect)*

Humans can gain social rank in different ways. In most other primates and social mammals, rank structure within groups is principally organized around dominance-rank differences established on the basis of competitive interactions involving agonism, force, aggression, intimidation, and violence (Bernstein, 1981; Hinde, 1974). In humans, however, the social organization of a collection of individuals is not simply an extension of these dominance hierarchies. For instance, we often seek out and defer-out of personal choice-to people who are particularly successful, skilled, and knowledgeable in locally valued domains (Boyd & Richerson, 1985; Boyd, Richerson, & Henrich, 2011; Henrich & Gil-White, 2001). These rank differences do not appear to be products of any agonistic coercion, fear, or imposition (as they are in dominance), but rather results from non-agonistic persuasion that is freely conferred. Emerging theoretical and empirical work delineates the distinction between these two forms of rank that operate in human societies. This work proposes that, unlike in other social mammals whose social organization is principally based on dominance (coercive capacity that derives from strength, threat, and intimidation), humans possess a separate pathway to social rank termed *prestige* (persuasive capacity that derives from valued skills, abilities, and knowledge; Cheng & Tracy, 2014; Cheng, Tracy, Foulsham, Kingstone, & Henrich, 2013; Henrich, 2016; Henrich & Gil-White, 2001; Maner, 2017). Empirically confirming this distinction, a substantial body of laboratory and field evidence indicates that prestige and dominance (a) can be distinguished by their ethological displays (e.g., postural and vocal cues and signals; Cheng, Tracy, & Henrich, 2010; Cheng, Tracy, Ho, & Henrich, 2016), motivational profiles (Case & Maner, 2014; Maner & Mead, 2010; Mead & Maner, 2012), and affective responses (Cheng et al., 2010); and (b) coexist to influence group decision-making and attention patterns in laboratory small groups (Cheng et al., 2013), naturalistic groups and teams in the field (Cheng et al., 2010; Redhead, Cheng, Driver, Foulsham, & O'Gorman, 2018), and even within the communities of people living in small-scale societies typified by highly egalitarian social norms (Garfield & Hagen, in press); and (c) lead to higher fitness outcomes, but via different mechanisms (Snyder, Kirkpatrick, & Barrett, 2008; von Rueden, Gurven, & Kaplan, 2011).

Recognizing this duality of social rank in human life opens up to a new vista of questions, including foremost: Does T regulate the pursuit and expression of both forms of social rank? The bulk of prior studies exploring the connection between T and social rank treat status as a unidimensional construct, operationalizing it as a confusing mix of both prestige and dominance. As discussed above, in these studies T effects are often explored in physically taxing sports competitions (e.g., wrestling, tennis) that emphasize both physical prowess (e.g., size and strength, agility, and endurance)—which may induce submission via perceived force and coercion (dominance)—and other game-relevant skills and abilities (e.g., planning, strategizing, technique) that may attract deference based on earned respect for perceived success and achievement (prestige). Even in studies of skill-based contests that lack physical confrontation (e.g., chess, tetris), this issue persists because direct competition with a sanctioned rival or enemy is likely to evoke a dominance psychology based on domination and subordination fueled by animosity and hostility, in addition to prestige stemming from greater intellectual skill.

Recent empirical work, however, is rectifying this conceptual ambiguity, and the latest findings from these efforts, when considered in conjunction with other existing evidence, are beginning to create a new picture that points to a role of T in both prestige and dominance rank competitions. Given that the focus on strictly prestige and T represents a stark departure from existing work on nonhumans (with its focus on agonistic dominance), here we focus on sketching the evidence that points to a link between T and prestige. The first line of evidence demonstrates that T levels predict the expression of behaviors that facilitate the pursuit of prestige (such as generosity; rather than dominance and aggression). That is, in sharp contrast to the early (but likely inaccurate) view that T causes hostile and aggressive behavior in humans, emerging evidence suggests that T may fuel prosocial preferences and behaviors, especially in contexts in which a prestige-based avenue to rank appears more viable or profitable (in terms of fitness gains). For example, in female communities-where highly dominant women may evoke particularly strong antidominance sentiments from subordinates (Benenson, 2013; Cashdan, 1995), thus making dominance a precarious long-term strategy in this context (Redhead et al., 2018)—a rise in T actually predicts greater affiliative interactions with other women (Casto & Edwards, 2016). In fact, directly linking T to prestige-based status, male and female athletes with higher T are not only seen as more skilled by teammates but also enjoy greater social popularity and connectedness-two proxies of high prestige (Edwards et al., 2006). In another study, salivary T is linked to reduced aggression and reactivity to angry faces in laboratory studies (Buades-Rotger et al., 2016). These findings dovetail with results from T administration studies, which reveal that an acute dose of T increases fairness in a bargaining game (Eisenegger et al., 2010), generosity toward those who are prosocial with them (reciprocity) (Boksem et al., 2013), and willingness to sanction norm-violators at a personal cost (Dreher et al., 2016).

The second line of evidence, which complements the research program (described above) on how T responds to contest outcomes, addresses whether and how T is modulated by experiences of gaining prestige (that is, winning and losing contests based solely on prestige, absent of dominance). In this vein, a recent study by our team examined T responses to changes in prestige ranking within a highly cooperative community. To unambiguously distinguish prestige from dominance, we focused on how T changes among individuals who attract substantial respect and admiration from members of their community, as a result of their earned merit and achievement, devoid of dominance, fear, or antagonism. Results show that men who achieve top ranks of the prestige hierarchy in the initial weeks of the group's formation show a rise in testosterone over the subsequent 2 months, whereas men with low prestige show a decline or little change in testosterone (Cheng, Kornienko, & Granger, 2018). These results converge with prior work demonstrating how winning competitions modulates T, but supply novel evidence that winning prestige, devoid of any dominance or antagonism, is sufficient to raise T levels. This hints at a possible role of T in facilitating the emergence and maintenance of prestige hierarchies.

In sum, recently emerging evidence suggests that T may be a candidate physiological mechanism that orchestrates both prestige- and dominance-seeking efforts (Eisenegger et al., 2011; Gray, McHale, & Carré, 2017). When the environment conspires against dominance and offers incentives for a prestige-based route to rank (such as in many contemporary workplaces), T may propel emotions (e.g., pride), motivations (e.g., affiliation versus aggression), and behaviors (e.g., generosity) that help sustain or increase an individual's prestige and influence (Cheng et al., 2010; Henrich, Chudek, & Boyd, 2015), all the time while aggression and a general inclination toward coercive tactics remain suppressed. Although this work is still in its infancy and a much larger database is needed, the empirical patterns available are consistent with the notion that T may, in some contexts, facilitate competition in prestige-based rank contests.

## 22.3 Current Status of Knowledge on Cortisol and Human Social Affiliation

In the next section, we shift our focus to cortisol (C) and affiliative relationships. Volumes of research have focused on the neuroendocrine underpinnings of the stress response, and the role of HPA axis and its end product cortisol in readying and facilitating the adaptation to chronic, unpredictable, and long-lasting stressors (e.g., Del Giudice, Ellis, & Shirtcliff, 2011; Gunnar & Quevedo, 2007; McEwen & Gianaros, 2010). Emerging conceptual and empirical efforts have been directed at describing the role of C in modulating social behavior. Here, we review evidence on

associations between social stress and salivary C in humans and propose that this evidence is best viewed in light of theorizing that emphasizes how C relates to social affiliation behavior that is directed at adaptation to stress, which among human primates (as well as nonhuman primates and other species, (Raulo & Dantzer, 2018), although the latter is beyond the scope of this review) unfolds as intricately connected with social interactions and embedded within social context. In constructing this empirical review, we again rely on extant reviews of empirical studies, and, when available, on meta-analyses to identify central themes from studies using salivary C. Using this approach, we identified five key insights into associations between C and social behavior. The major take-home points from this section of the review are that:

- Elevated C is associated with inhibition and withdrawal from social relationships and anxiety, loneliness, social isolation, social rejection, and social status threat.
- But elevated C can also increase social affiliation as a means of stress reduction, and serve as a social buffering mechanism within the context of parental relationships.
- Distinguishing between stressors that are endogenous (i.e., internal) and exogenous (i.e., external) to social relationship may help delineate patterns of cortisolsocial behavior links.
- C response is dampened in the presence of conspecifics who provide social buffering effects when the stressor is exogenous.
- The social nature and intensity of stressors moderate C response and its association with social behavior.

### 22.3.1 Cortisol Underpins Social Behavior as a Part of the Stress Response

C, a glucocorticoid, is the primary end product of activity of the HPA axis in humans (Chrousos & Gold, 1992; see Chap. 5). Cortisol levels trend higher when individuals (a) appraise a situation to be challenging, uncertain, and intense, and (b) experience rumination and social status threat (Denson, Spanovich, & Miller, 2009; Dickerson, 2008). Short-term elevation of cortisol is considered to be adaptive in novel or dynamic social environments (Sapolsky et al., 2000), whereas prolonged activation has the potential to translate into cumulative wear and tear on many biological systems with downstream consequences for health (McEwen & Gianaros, 2010).

According to the integrated specificity model of stress (Kemeny, 2003; Lazarus & Folkman, 1984; Weiner, 1992), specific stressors and their cognitive appraisals initiate a psychobiological stress response, including the mobilization of emotional, motivational, and physiological systems. Perceived control over stressors instantiates *defeat* and *defense* strategies as a part of the integrated stress response profile. Threats to one's well-being that are appraised as uncontrollable and outside of the scope of one's coping resources may initiate *defeat or disengagement responses*.

Defeat responses drive HPA axis activity and associated distress, withdrawal, and depressed affect (Chrousos & Gold, 1992). Research has shown that individual differences in C levels are linked with social withdrawal, inhibition, and anxiety (e.g., Kagan, Reznick, & Snidman, 1987; Shoal, Giancola, & Kirillova, 2003; Smider et al., 2002).

Stressors appraised as controllable and within one's coping resources lead to *defense or engagement responses* including fight or flight responses, which are mediated by the activity of autonomic nervous system cascades involving respective upregulation of sympathetic and downregulation of parasympathetic branches (Koolhaas & Bohus, 1989). Stressful conditions, in which competition and dominance dynamics are apparent, especially under conditions of instability of a social hierarchy, have been linked to increased T levels when an individual engages in active coping with a challenge; by contrast, T levels tend to plummet when an individual is passively or reactively coping with a challenge (Archer, 2006; Mehta & Josephs, 2010; Salvador & Costa, 2009; Schoofs & Wolf, 2011). Another line of research suggests that activation of HPA axis is associated with the mobilization of coping resources and increased sensitivity to social cues and feedback (Del Giudice et al., 2011), which may be beneficial for an individual who occupies a position of high social status, in part because being at the top of the group hierarchy may require the capacity to detect and respond to threats to one's social standing.

Yet another pattern through which cortisol might be associated with social behavior involves the "tend-and-befriend" model as an alternative coping response to stress. Affiliation with others under stress is a protective mechanism to restore safety and avert threats (Taylor, 2011). Given the prevalence of gender-based division of labor in human history, in which men were primarily responsible for hunting and group protection and women for gathering and child-rearing, women's stress response may have evolved to not only protect oneself but one's offspring during times of stress. Taylor et al. (2000) and Taylor (2006) proposed that, particularly for women, fight or flight may not be the most adaptive response compared to tend or befriend. Here, "tending" involves nurturant activities designed to promote safety and reduce the distress of the self and offspring, whereas "befriending" is the existence and use of social networks that may aid in these processes (Taylor et al., 2000). The "tend-and-befriend" model posits that individuals, especially women, may form tight and/or extensive social ties and seek out friends in times of stress, who provide them with social support and help buffer against the deleterious effects of stress. Indeed, tending and befriending, as in turning to others for support and help, have been shown to be an effective stress coping strategy (e.g., Tamres, Janicki, & Helgeson, 2002). But it is noteworthy that both men and women turn to others for help under stress, and other lines of research guided by evolutionary logic suggest that men are also likely to create more extensive networks and befriend more non-kin peers given their greater reliance on coalitional building during hunting and group protection (Benenson, 2014).

#### 22.3.1.1 Social Context Moderates Stress Response and Adaptation

Adapting to the trials and tribulations of everyday life may sometimes occur in social isolation, but, among inherently social humans, it is also common for these processes to unfold in the context of networked social relationships (i.e., family, friends). Living in social groups affords individuals many advantages and theorists suggest that the nature and complexity of components of the human central nervous system have evolved to meet the demands of living in large groups (e.g., processing ambiguous social information; Chang et al., 2013; Seyfarth & Cheney, 2013; Silk, 2007). Not surprisingly, individual differences in the activity and regulation of the HPA axis are associated with subjective experiences created throughout social interactions with group members (e.g., social evaluation and status threat, novelty, unpredictability; Denson et al., 2009; Dickerson & Kemeny, 2004). The biobehavioral associations between hormones and social behavior are shaped not only by the nature of a stressor (status-related, requiring an extended effort) and its cognitive appraisal (Denson et al., 2009), but also by its social context (e.g., quality of family relationships; Booth, Johnson, Granger, Crouter, & McHale, 2003).

When considering the adaption to stressors within a context of social relationships, it is useful to distinguish between whether the stressor to which an individual is responding occurs within the context of a social relationship (i.e., stressor is endogenous to a relationship), or if the stressor occurs outside of the context of a social relationship (i.e., stressor is exogenous to a relationship). Social support or buffering effects on HPA activity are typically documented with stressors that are exogenous to one's relationship (i.e., public speaking or some other external event). For example, one study showed that the presence of a parent or a friend was associated with faster HPA axis recovery after a public speaking task, suggesting a social buffering effect (Hostinar, Johnson, & Gunnar, 2015). However, a closer look at the accumulating evidence on the moderating role of social context hints at how potent stressors may emerge as a function of one's social relationships (i.e., endogenous stressors), with interpersonal stressors of poor relationship quality, high degree of conflict and negativity, and social rejection exerting an influence on neuroendocrine processes and social behavior. We next briefly consider these two types of stressors.

Stressors that Are Endogenous to Social Relationships

**Social Rejection and Social Status Threat** As previously discussed, higher C levels are linked to fear of social rejection and losing social status, acceptance, and esteem. These patterns have been robustly established among children (Gunnar, Sebanc, Tout, Donzella, & van Dulmen, 2003), adolescents (Adam, 2006; Blackhart, Eckel, & Tice, 2007), and adults (Dickerson, 2008; Dickerson & Kemeny, 2004; Dickerson & Zoccola, 2013).

Loneliness Being isolated from the social group is a major stressor, and neuroendocrine and physiological systems link loneliness with heightened activity of the HPA axis (Adam, Hawkley, Kudielka, & Cacioppo, 2006; Cacioppo, Capitanio, & Cacioppo, 2014). Prolonged experiences of loneliness have detrimental health outcomes, including diminished cardiovascular health, immunity, sleep quality, and mental health (Pressman et al., 2005; Valtorta, Kanaan, Gilbody, Ronzi, & Hanratty, 2016). In contrast, transient feelings of loneliness serve an adaptive signaling function and promote the restoration of the basic belongingness need by seeking and renewing social relationships (Cacioppo et al., 2014). It is thought that feelings of loneliness activate the self-preservation system and its integral componentheightened vigilance to social threat (Cacioppo et al., 2014). A critical physiological marker of social threat is the activity of HPA axis and its end product C (Dickerson, 2008). Indeed, research has linked loneliness to increased HPA activity (Adam et al., 2006; Cacioppo et al., 2002; Doane & Adam, 2010; Glaser, Kiecolt-Glaser, Speicher, & Holliday, 1985; Steptoe, Owen, Kunz-Ebrecht, & Brydon, 2004). Whereas cortisol is a stress hormone, it can serve as an adaptive function of energy mobilization (Del Giudice et al., 2011), which could support the development of social connection for a lonely individual.

**Poor Relationship Quality, Negativity, and Conflict** Social relationships may sometimes be the source of conflict, strain, and discord, which qualifies them to be salient psychosocial stressors with negative consequences for health (e.g., Newsom, Mahan, Rook, & Krause, 2008). Indeed, empirical evidence suggests that negativity and aversive interactions within close relationships are significant stressors (Rook, 1984, 2001) and have detrimental effects on health (Kiecolt-Glaser & Newton, 2001) and stress physiology (Timmons, Margolin, & Saxbe, 2015). A recent review of 18 studies reveals cortisol coregulation within romantic or marital dyads, and moreover joint increases in cortisol levels predict poorer relationship quality and higher levels of conflict (Timmons et al., 2015).

Attunement on Cortisol in Social Relationships Group living and social ties that connect individual members within a group are viewed as crucial adaptations contributing to the fitness of human and nonhuman primates (e.g., Silk, 2007). Researchers have proposed that this adaptive nature of groups emerges through processes of *bio-behavioral synchrony* (Feldman, 2015) or *attunement* (Granger et al., 2012), defined as the temporal, ongoing coordination of biological, and behavioral processes among members of a social group. Empirical evidence documents physiological attunement for a variety of dyadic social relationships, including parent–child bonds (Booth et al., 2003; Sethre-Hofstad, Stansbury, & Rice, 2002), married or dating couples (Timmons et al., 2015), and friendship dyads (Rankin, Swearingen-Stanborough, Granger, & Byrd-Craven, 2018). Moving beyond the dyad as the unit of analysis, physiological attunement has been reported even among small family groups (Booth et al., 2000). A recent meta-analysis of 29 laboratory and 16 ecological studies of romantic and family dyads suggests robust adrenocortical attunement among dyad members (Ha et al., 2018).

#### Stressors that Are Exogenous to Social Relationships

When adapting to exogenous stressors—external to one's social relationship individuals may draw on social connections, which provide social buffering effects on adrenocortical activity. In such circumstances, as a prominent model—the social buffering hypothesis—posits, social support derived from one's social relationships serves protective effects by attenuating the physiological stress response (Carter, 1998; Feldman, 2015; Gunnar & Hostinar, 2015; Hostinar, Sullivan, & Gunnar, 2014). This hypothesis has received some support within the context of parent—child relationships (e.g., Gunnar & Quevedo, 2007). However, a recent meta-analysis of 38 studies failed to find an overall non-zero effect for the association between parental warmth and offspring HPA axis basal levels, reactivity, or recovery (Hackman, O'Brien, & Zalewski, 2018). Upon examination of moderators, it appeared that parental warmth was protective against reactivity but not recovery in laboratory tasks in which social status threat was acute. Hackman et al. concluded that this might have implications for children's appraisal of stressors.

Interestingly, emerging evidence suggests that parental support does not effectively promote recovery of the HPA axis after a public speaking task during adolescence, whereas friend support does (Hostinar et al., 2015). Furthermore, the presence of a friend appears to have dampening effects on the reactivity of the HPA axis to negative social experiences and exclusion in naturalistic ecologies (Adams, Santo, & Bukowski, 2011; Peters, Riksen-Walraven, Cillessen, & de Weerth, 2011) and the laboratory (Calhoun et al., 2014).

In summary, the extensive body of theoretical and empirical work points to the vital role that C may play in the modulation of social behavior. The emerging patterns of this association are not linear and straightforward. On the one hand, elevated C is associated with reduced social affiliation—social inhibition, with-drawal from social relationships, social isolation, social rejection, and social status threat. On the other hand, elevated C can also increase social affiliation as a means of stress reduction, where social support and buffering mechanisms operate in the context of a social relationship (e.g., parent–child relationship) and increased sociality is associated with downregulation of HPA axis activity. Another theme that is apparent across the vast corpus of evidence on cortisol-social affiliation link is that features of the social context moderate C response and its association with social behavior.

# 22.4 Methodological Opportunities, Challenges, and Considerations in the Study of Salivary Bioscience and Human Social Behavior

As reviewed above, in the last several decades, a large scientific enterprise has emerged to lay the foundation for understanding endocrinology and its relation with social relationships in humans and nonhuman animals. Despite the progress made, however, many key puzzles in human social behavioral endocrinology remain to be solved and a number of important discoveries are, in all likelihood, yet to be made. Here we propose three methodological recommendations to facilitate a greater understanding of the complex interplay between neurobiology and social behavior: (1) conduct field studies; (2) sample diverse, non-WEIRD populations; and (3) extend focus to social networks and communities, beyond individuals and dyads.

# 22.4.1 Go Wild! The Importance of Studying Neurobiology and Human Social Behavior in the Field and Outside of the Laboratory

As our review above highlights, scientific inquiry into the neurobiological underpinnings of human social dynamics has proliferated from an exceptionally strong integration of extensive field and laboratory evidence. Insofar that the combined use of both laboratory and field studies will continue to be paramount for developing comprehensive models of neurobiology and social dynamics, one important direction for future work is to further expand the existing corpus of field studies. In the branch of work on cortisol (Saxbe, 2008), for instance, giant strides have been made over the last two decades, owing in part to an increasing shift in focus from laboratory-based stress induction methodologies (reviewed in Dickerson & Kemeny, 2004) to field research on everyday stress and coping. The tremendous promise and value of studying neurobiology "in the wild" is strikingly demonstrated by a recent meta-analysis of T effects. After surveying the last 35 years of research on the effects of competition outcome on T responses, the authors concluded that "the strength of the 'winner-loser' effect depended on the location of the competition, whereby the effect was much stronger in studies conducted outside the lab... compared to studies conducted in the lab" (Geniole et al., 2017, p. 47). "Much stronger" is perhaps an understatement; the average effect is six times stronger in the field as it is in the laboratory. Although the basis for why these T effects are larger in the field is not well understood, a primary factor, that is suspect is the greater potency of the social experience in the field (e.g., greater psychological investment in winning in real life compared to a laboratory game; Geniole et al., 2017; Oliveira, 2004). Put simply,

there are simply few laboratory analogs capable of simulating the powerful experience of human social interactions as in real life. There are, of course, an array of other important reasons for undertaking field research—from establishing ecological validity to exploring questions that cannot be answered in the laboratory (e.g., How does social rank alter T longitudinally? How does reproductive behavior change hormones? What effect does basal HPA axis activity have on primate health? Cheng et al., 2018; Gray et al., 2017; Sapolsky, 2005). Nevertheless, on a practical front the unparalleled potency of human social relationships and experiences in real life, and their powerful effects on endocrinology, provide unrivaled research opportunities.

### 22.4.2 Sample Diverse Populations, Especially non-WEIRD Individuals

Across the behavioral sciences there is growing interest in identifying aspects of human nature that are universal as well as those that are culturally variable, using comparative research with diverse societies, beyond the traditional WEIRD (Western Educated Industrialized Rich Democratic) samples on which much of existing empirical foundations is built (Apicella & Barrett, 2016; Henrich, Heine, & Norenzayan, 2010). Behavioral endocrinology researchers, too, are responding to this call; an emerging generation of comparative research programs is beginning to shed new light on the ways in which the interplay between hormones and behavior are similar or variable across cultures. Among these efforts, for example, is Trumble et al.' (2012) recent study of the Tsimane, forager-horticulturalists of the Bolivian Amazon, which reveals evidence of the same pattern of a competition-induced T increase in men typically found in WEIRD samples.

These results contribute a crucial data point to the existing empirical database that is heavily skewed toward sampling men in industrialized societies, who, in fact, have an unusually high level of T across all ages (Bribiescas, 1996), possibly owing to the low energetic and pathogenic stress typified by industrialized settings. Thus, evidence of a qualitatively similar competition-induced increase in men in nonindustrialized societies, where investment in exaggerated T-related faculties may be too costly and is thus reflected in a lower basal T level in males, is crucial and offers some suggestive preliminary evidence that perhaps the social modulation of T effects that are relatively well established in industrialized contexts may, in fact, generalize beyond the WEIRD contexts studied and apply species-wide. Other similar efforts include work that investigates, for instance, how T responds to experiences of challenge, such as hunting excursions and actual kills in Tsimane and !Kung San men (Jaeggi, Trumble, Kaplan, & Gurven, 2015; Trumble, Smith, O'Connor, Kaplan, & Gurven, 2014; Worthman & Konner, 1987), and paternal caregiving among East African foragers and pastoralists (Muller, Marlowe, Bugumba, & Ellison, 2009). As these efforts illustrate, comparative research on behavioral endocrinology with diverse societies, while challenging, will likely occupy an increasingly central role for generating broad insights into the complex nature of hormone-behavior interactions in our species.

# 22.4.3 Contributions of Social Network Analysis to Study the Social System in Its Entirety, Beyond Individuals and Dyads

Research to date has advanced our understanding of hormone regulation of social behavior considered at the level of an individual, dyads, and social groups. A key limitation of this research when it comes to examining social groups and communities is that it has predominantly relied on aggregate composites of group processes and ignoring the role that social network structure and dynamics play for hormone-social behavior associations (for an exception see research with nonhuman primate dominance hierarchies; Sapolsky, 2005). Social networks represent the structures and dynamics of group living and social connections among individuals in a group are central to understanding social behavior and context because they govern the ways in which relational provisions such as information, resources, and support are distributed (for reviews, see Borgatti, Mehra, Brass, & Labianca, 2009; Kadushin, 2012). As such social networks emerge as a result of an individual's social behavior in a group and influence psychological and neuroendocrine processes (for reviews, see Berkman, Glass, Brissette, & Seeman, 2000; Crosier, Webster, & Dillon, 2012).

Social network theory and analytical tools enable pursuing several innovative research questions by examining social systems in their entirety (e.g., communities and networks), beyond individuals and dyads. The first set of questions focuses on the understanding of hormone associations with network position, which is derived from nominations collected from individuals (i.e., egos) and their group members (i.e., alters) within a defined social group. Complete network data, referring to multi-informant assessment of network ties (O'Mailey & Marsden, 2008; Wasserman & Faust, 1994), allow the consideration of directed and mutual relationships within a social system. An individual's outgoing ties depict social network activity or gregariousness, whereas incoming ties describe social popularity and status (Wasserman & Faust, 1994). Social network density, describing the degree of interconnectedness among one's friends, has implications for the flow of social support and stress-buffering processes (Walker, Wasserman, & Wellman, 1993) and, therefore, may have direct and moderating effects on associations between social stressors and cortisol. An individual's network centrality is measured by

outgoing direct and indirect ties to all other members of a community and has implications for access to resources and information (Borgatti et al., 2009) and likely serves a stress-buffering effect.

Emerging studies of nonhuman and human primates suggest that hormones are associated with social network position and structure. Specifically, high-ranking free-ranging female macaques were shown to have lower glucocorticoid levels when their association networks were smaller and more focused, as indexed by a lower number of outgoing connections (Brent, Semple, Dubuc, Heistermann, & MacLarnon, 2011). Among female nursing students (Kornienko, Clemans, Out, & Granger, 2013; Kornienko, Clemans, Out, & Granger, 2013; Kornienko, Clemans, Out, & Granger, 2016), salivary C levels were also inversely associated with gregariousness levels; these findings are in line with prior research documenting the impact of social isolation on HPA axis activity.

Because social ties within a group are not formed and dissolved randomly, the second set of questions that could be addressed with the use of SNA approaches focuses on examining how hormones are associated with how social network structures are being created. Social network selection refers to understanding changes in networks based on factors that include (a) individual characteristics (e.g., hormone levels) that affect the tendency to form ties and (b) network structural processes (e.g., popularity, transitivity), reflecting how connections between individuals depend on the nature of their ties with other members of a group. Networks research has shown that to obtain unbiased estimates of how hormone concentrations contribute to network selection; thus, we need to statistically control for alternative network structural processes using social network modeling approaches (Snijders, 2011).

A recent investigation explored the role of cortisol and testosterone levels in predicting friendship tie maintenance and creation over time in a social network of members of a collegiate marching band (Kornienko, Schaefer, Weren, Hill, & Granger, 2016). The findings revealed that over time, individuals with lower cortisol levels were more likely to maintain friendships, and those with higher cortisol levels were more likely to create new ties. In contrast, individuals with higher testosterone levels were more likely to maintain existing friendships and less likely to create new relationships. The reader is referred to Figs. 22.1 and 22.2 for illustrations of contemporaneous associations between social network structure and salivary levels of cortisol and testosterone in a large mixed-gender organization of a marching band. This work points to exciting new directions to discover how hormones are associated with social behavior through which social relationships among group members are initiated, maintained, and lost in order to advance our understanding the structure and function of human social ecology for individual behavior and adaptation (for a review, see Pinter-Wollman et al., 2014).



**Fig. 22.1** Visual representation of friendship network and salivary cortisol levels. Links between nodes represent directed friendship ties, arrows omitted to improve visual layout. Node size corresponds to individual's salivary C level, which was multiplied by a constant of 7.5 (larger nodes = higher levels of C). Node color denotes gender (white = male; gray = female)

 $\circ$ 



**Fig. 22.2** Visual representation of friendship network and salivary testosterone levels. Links between nodes represent directed friendship ties, arrows omitted to improve visual layout. Node size corresponds to individual's salivary T level, which was divided by a constant of 50 (larger nodes = higher levels of T). Node color denotes gender (white = male; gray = female)

#### References

- Adam, E. K. (2006). Transactions among adolescent trait and state emotion and diurnal and momentary cortisol activity in naturalistic settings. *Psychoneuroendocrinology*, 31, 664–679. https://doi.org/10.1016/j.psyneuen.2006.01.010
- Adam, E. K., Hawkley, L. C., Kudielka, B. M., & Cacioppo, J. T. (2006). Day-to-day dynamics of experience–cortisol associations in a population-based sample of older adults. *Proceedings of* the National Academy of Sciences of the U S A, 103, 17058–17063.
- Adams, R. E., Santo, J. B., & Bukowski, W. M. (2011). The presence of a best friend buffers the effects of negative experiences. *Developmental Psychology*, 47(6), 1786.
- Aikey, J. L., Nyby, J. G., Anmuth, D. M., & James, P. J. (2002). Testosterone rapidly reduces anxiety in male house mice (Mus musculus). *Hormones and Behavior*, 42(4), 448–460.
- Andrew, R. J., & Rogers, L. J. (1972). Testosterone, search behaviour and persistence. *Nature*, 237 (5354), 343–345. https://doi.org/10.1038/237343a0
- Anestis, S. F. (2006). Testosterone in juvenile and adolescent male chimpanzees (Pan troglodytes): Effects of dominance rank, aggression, and behavioral style. *American Journal of Physical Anthropology*, 130(4), 536–545. https://doi.org/10.1002/ajpa.20387
- Anonymous. (1970). Effects of sexual activity on beard growth in man. *Nature*, 226(5248), 869–870. https://doi.org/10.1038/226869a0
- Apicella, C. L., & Barrett, H. C. (2016). Cross-cultural evolutionary psychology. Current Opinion in Psychology, 7, 92–97. https://doi.org/10.1016/j.copsyc.2015.08.015
- Apicella, C. L., Carré, J. M., & Dreber, A. (2015). Testosterone and economic risk taking: A review. Adaptive Human Behavior and Physiology, 1(3), 358–385. https://doi.org/10.1007/s40750-014-0020-2
- Apicella, C. L., Dreber, A., Campbell, B., Gray, P. B., Hoffman, M., & Little, A. C. (2008). Testosterone and financial risk preferences. *Evolution and Human Behavior*, 29(6), 384–390. https://doi.org/10.1016/j.evolhumbehav.2008.07.001
- Archer, J. (1977). Testosterone and persistence in mice. Animal Behaviour, 25(2), 479–488. https:// doi.org/10.1016/0003-3472(77)90023-9
- Archer, J. (1991). The influence of testosterone on human aggression. British Journal of Psychology, 82(1), 1–28. https://doi.org/10.1111/j.2044-8295.1991.tb02379.x
- Archer, J. (2004). Sex differences in aggression in real-world settings: A meta-analytic review. *Review of General Psychology*, 8(4), 291–322. https://doi.org/10.1037/1089-2680.8.4.291
- Archer, J. (2006). Testosterone and human aggression: An evaluation of the challenge hypothesis. *Neuroscience and Biobehavioral Reviews*, 30(3), 319–345. https://doi.org/10.1016/j.neubiorev. 2004.12.007
- Archer, J., Birring, S. S., & Wu, F. C. W. (1998). The association between testosterone and aggression among young men: Empirical findings and a meta-analysis. *Aggressive Behavior*, 24(6), 411–420. https://doi.org/10.1002/(SICI)1098-2337(1998)24:6<411::AID-AB2>3.0. CO;2-9
- Archer, J., & Coyne, S. M. (2005). An integrated review of indirect, relational, and social aggression. *Personality and Social Psychology Review*, 9(3), 212–230. https://doi.org/10. 1207/s15327957pspr0903\_2
- Archer, J., Graham-Kevan, N., & Davies, M. (2005). Testosterone and aggression: A reanalysis of Book, Starzyk, and Quinsey's (2001) study. *Aggression and Violent Behavior*, 10(2), 241–261. https://doi.org/10.1016/j.avb.2004.01.001
- Arslan, M., Akhtar, F. B., & Nieschlag, E. (1984). Salivary testosterone levels in normal and testosterone treated monkeys. *Journal of Steroid Biochemistry*, 21, 461–464. https://doi.org/10. 1016/0022-4731(84)90312-1
- Assari, S., Caldwell, C. H., & Zimmerman, M. A. (2014). Sex differences in the association between testosterone and violent behaviors. *Trauma Monthly*, 19(3), e18040. https://doi.org/ 10.5812/traumamon.18040

Batrinos, M. L. (2012). Testosterone and aggressive behavior in man. International Journal of Endocrinology and Metabolism, 10(3), 563–568. https://doi.org/10.5812/ijem.3661

Beach, F. A. (1948). Hormones and behavior. New York, NY: Paul Hoeber.

- Beehner, J. C., Bergman, T. J., Cheney, D. L., Seyfarth, R. M., & Whitten, P. L. (2006). Testosterone predicts future dominance rank and mating activity among male chacma baboons. *Behavioral Ecology and Sociobiology*, 59(4), 469–479. https://doi.org/10.1007/s00265-005-0071-2
- Beeman, E. A. (1947). The relation of the interval between castration and first encounter to the aggressive behavior of mice. *The Anatomical Record*, *99*(4), 570.
- Behringer, V., & Deschner, T. (2017). Non-invasive monitoring of physiological markers in primates. *Hormones and Behavior*, 91, 3–18. https://doi.org/10.1016/j.yhbeh.2017.02.001
- Behringer, V., Deschner, T., Deimel, C., Stevens, J. M. G., & Hohmann, G. (2014). Age-related changes in urinary testosterone levels suggest differences in puberty onset and divergent life history strategies in bonobos and chimpanzees. *Hormones and Behavior*, 66(3), 525–533. https://doi.org/10.1016/j.yhbeh.2014.07.011
- Beletsky, L. D., Orians, G. H., & Wingfield, J. C. (1992). Year-to-year patterns of circulating levels of testosterone and corticosterone in relation to breeding density, experience, and reproductive success of the polygynous red-winged blackbird. *Hormones and Behavior*, 26(3), 420–432. https://doi.org/10.1016/0018-506X(92)90011-J
- Benenson, J. F. (2013). The development of human female competition: Allies and adversaries. *Philosophical Transactions of the Royal Society B*, 368(1631), 20130079. https://doi.org/10. 1098/rstb.2013.0079
- Benenson, J. F. (2014). *Warriors and worriers: The survival of the sexes*. Oxford: Oxford University Press.
- Berkman, L. F., Glass, T., Brissette, I., & Seeman, T. E. (2000). From social integration to health: Durkheim in the new millennium. Social Science and Medicine, 51, 843–857.
- Bernhardt, P. C., Dabbs, J. M., Jr., Fielden, J. A., & Lutter, C. D. (1998). Testosterone changes during vicarious experiences of winning and losing among fans at sporting events. *Physiology* and Behavior, 65(1), 59–62. https://doi.org/10.1016/S0031-9384(98)00147-4
- Bernstein, I. S. (1981). Dominance: The baby and the bathwater. *Behavioral and Brain Sciences*, 4 (3), 419–429.
- Blackhart, G. C., Eckel, L. A., & Tice, D. M. (2007). Salivary cortisol in response to acute social rejection and acceptance by peers. *Biological Psychology*, 75(3), 267–276.
- Boksem, M. A. S., Mehta, P. H., den Bergh, B. V., van Son, V., Trautmann, S. T., Roelofs, K., ... Sanfey, A. G. (2013). Testosterone inhibits trust, but promotes reciprocity. *Psychological Science*, 24(11), 2306–2314. https://doi.org/10.1177/0956797613495063
- Booth, A., Carver, K., & Granger, D. A. (2000). Biosocial perspectives on the family. *Journal of Marriage and Family*, 62(4), 1018–1034. https://doi.org/10.1111/j.1741-3737.2000.01018.x
- Book, A. S., Starzyk, K. B., & Quinsey, V. L. (2001). The relationship between testosterone and aggression: A meta-analysis. Aggression and Violent Behavior, 6(6), 579–599. https://doi.org/ 10.1016/S1359-1789(00)00032-X
- Booth, A., Granger, D. A., Mazur, A., & Kivlighan, K. T. (2006). Testosterone and social behavior. Social Forces, 85(1), 167–191. https://doi.org/10.1353/sof.2006.0116
- Booth, A., Johnson, D. R., Granger, D. A., Crouter, A. C., & McHale, S. (2003). Testosterone and child and adolescent adjustment: The moderating role of parent-child relationships. *Developmental Psychology*, 39(1), 85.
- Booth, A., Mazur, A. C., & Dabbs, J. M. (1993). Endogenous testosterone and competition: The effect of "fasting". *Steroids*, 58(8), 348–350. https://doi.org/10.1016/0039-128X(93)90036-M
- Booth, A., Shelley, G., Mazur, A., Tharp, G., & Kittok, R. (1989). Testosterone, and winning and losing in human competition. *Hormones and Behavior*, 23(4), 556–571. https://doi.org/10.1016/ 0018-506X(89)90042-1
- Borgatti, S. P., Mehra, A., Brass, D. J., & Labianca, G. (2009). Network analysis in the social sciences. Science, 323, 892–895. https://doi.org/10.1126/science.1165821

- Boyce, W. T., Champoux, M., Suomi, S. J., & Gunnar, M. R. (1995). Salivary cortisol in nurseryreared rhesus monkeys: Reactivity to peer interactions and altered circadian activity. *Developmental Psychobiology*, 28(5), 257–267. https://doi.org/10.1002/dev.420280502
- Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago, IL: University of Chicago Press.
- Boyd, R., Richerson, P. J., & Henrich, J. (2011). The cultural niche: Why social learning is essential for human adaptation. *Proceedings of the National Academy of Sciences*, 108, 10918–10925. https://doi.org/10.1073/pnas.1100290108
- Brain, P. F., & Haug, M. (1992). Hormonal and neurochemical correlates of various forms of animal "aggression". *Psychoneuroendocrinology*, 17(6), 537–551. https://doi.org/10.1016/ 0306-4530(92)90014-X
- Brent, L. J. N., Semple, S., Dubuc, C., Heistermann, M., & MacLarnon, A. (2011). Social capital and physiological stress levels in free-ranging adult female rhesus macaques. *Physiology and Behavior*, 102, 76–83. https://doi.org/10.1016/j.physbeh.2010.09.022
- Bribiescas, R. G. (1996). Testosterone levels among Aché hunter-gatherer men. *Human Nature*, 7 (2), 163–188. https://doi.org/10.1007/BF02692109
- Buades-Rotger, M., Engelke, C., Beyer, F., Keevil, B. G., Brabant, G., & Krämer, U. M. (2016). Endogenous testosterone is associated with lower amygdala reactivity to angry faces and reduced aggressive behavior in healthy young women. *Scientific Reports*, 6, 38538. https:// doi.org/10.1038/srep38538
- Cacioppo, S., Capitanio, J. P., & Cacioppo, J. T. (2014). Toward a neurology of loneliness. Psychological Bulletin, 140, 1464–1504. https://doi.org/10.1037/a0037618
- Cacioppo, J. T., Hawkley, L. C., Berntson, G. G., Ernst, J. M., Gibbs, A. C., Stickgold, R., & Hobson, J. A. (2002). Do lonely days invade the nights? Potential social modulation of sleep efficiency. *Psychological Science*, 13(4), 384–387.
- Calhoun, C. D., Helms, S. W., Heilbron, N., Rudolph, K. D., Hastings, P. D., & Prinstein, M. J. (2014). Relational victimization, friendship, and adolescents' hypothalamic–pituitary–adrenal axis responses to an in vivo social stressor. *Development and Psychopathology*, 26, 605–618. https://doi.org/10.1017/S0954579414000261
- Cant, M. A., English, S., Reeve, H. K., & Field, J. (2006). Escalated conflict in a social hierarchy. Proceedings of the Royal Society of London B: Biological Sciences, 273(1604), 2977–2984. https://doi.org/10.1098/rspb.2006.3669
- Carré, J. M. (2009). No place like home: Testosterone responses to victory depend on game location. American Journal of Human Biology, 21(3), 392–394. https://doi.org/10.1002/ajhb. 20867
- Carré, J. M., & McCormick, C. M. (2008). Aggressive behavior and change in salivary testosterone concentrations predict willingness to engage in a competitive task. *Hormones and Behavior*, 54 (3), 403–409. https://doi.org/10.1016/j.yhbeh.2008.04.008
- Carré, J. M., McCormick, C. M., & Hariri, A. R. (2011). The social neuroendocrinology of human aggression. *Psychoneuroendocrinology*, 36(7), 935–944. https://doi.org/10.1016/j.psyneuen. 2011.02.001
- Carré, J. M., & Olmstead, N. A. (2015). Social neuroendocrinology of human aggression: Examining the role of competition-induced testosterone dynamics. *Neuroscience*, 286, 171–186. https://doi.org/10.1016/j.neuroscience.2014.11.029
- Carré, J. M., & Putnam, S. K. (2010). Watching a previous victory produces an increase in testosterone among elite hockey players. *Psychoneuroendocrinology*, 35(3), 475–479. https:// doi.org/10.1016/j.psyneuen.2009.09.011
- Carter, C. S. (1998). Neuroendocrine perspective on social attachment and love. *Psychoneuroendocrinology*, 23, 779–818.
- Case, C. R., & Maner, J. K. (2014). Divide and conquer: When and why leaders undermine the cohesive fabric of their group. *Journal of Personality and Social Psychology*, 107(6), 1033–1050. https://doi.org/10.1037/a0038201
- Cashdan, E. (1995). Hormones, sex, and status in women. *Hormones and Behavior*, 29(3), 354–366. https://doi.org/10.1006/hbeh.1995.1025

- Casto, K. V., & Edwards, D. A. (2016). Testosterone and reconciliation among women: Aftercompetition testosterone predicts prosocial attitudes towards opponents. *Adaptive Human Behavior and Physiology*, 2(3), 220–233. https://doi.org/10.1007/s40750-015-0037-1
- Cavigelli, S. A., & Pereira, M. E. (2000). Mating season aggression and fecal testosterone levels in male ring-tailed lemurs (Lemur catta). *Hormones and Behavior*, 37(3), 246–255. https://doi.org/ 10.1006/hbeh.2000.1585
- Celec, P., Ostatníková, D., & Hodosy, J. (2015). On the effects of testosterone on brain behavioral functions. *Frontiers in Neuroscience*, 9, 12. https://doi.org/10.3389/fnins.2015.00012
- Chang, S. W. C., Brent, L. J. N., Adams, G. K., Klein, J. T., Pearson, J. M., Watson, K. K., & Platt, M. L. (2013). Neuroethology of primate social behavior. *PNAS*, 110(S2), 10387–10394.
- Cheng, J. T., Kornienko, O., & Granger, D. A. (2018). Prestige in a large-scale social group predicts longitudinal changes in testosterone. *Journal of Personality and Social Psychology*, 114(6), 924–944. https://doi.org/10.1037/pspi0000126
- Cheng, J. T., & Tracy, J. L. (2014). Toward a unified science of hierarchy: Dominance and prestige are two fundamental pathways to human social rank. In J. T. Cheng, J. L. Tracy, & C. Anderson (Eds.), *The psychology of social status* (pp. 3–27). New York, NY: Springer. https://doi.org/10. 1007/978-1-4939-0867-7\_1
- Cheng, J. T., Tracy, J. L., Foulsham, T., Kingstone, A., & Henrich, J. (2013). Two ways to the top: Evidence that dominance and prestige are distinct yet viable avenues to social rank and influence. *Journal of Personality and Social Psychology*, 104(1), 103–125. https://doi.org/10. 1037/a0030398
- Cheng, J. T., Tracy, J. L., & Henrich, J. (2010). Pride, personality, and the evolutionary foundations of human social status. *Evolution and Human Behavior*, 31(5), 334–347. https://doi.org/10. 1016/j.evolhumbehav.2010.02.004
- Cheng, J. T., Tracy, J. L., Ho, S., & Henrich, J. (2016). Listen, follow me: Dynamic vocal signals of dominance predict emergent social rank in humans. *Journal of Experimental Psychology: General*, 145(5), 536–547. https://doi.org/10.1037/xge0000166
- Chrousos, G. P., & Gold, P. W. (1992). The concepts of stress and stress system disorders: Overview of physical and behavioral homeostasis. *Journal of American Medical Association*, 267, 1244–1252. https://doi.org/10.1001/jama.1992.03480090092034
- Clotfelter, E. D., & Paolino, A. D. (2003). Bystanders to contests between conspecifics are primed for increased aggression in male fighting fish. *Animal Behaviour*, 66(2), 343–347. https://doi. org/10.1006/anbe.2003.2227
- Coates, J. M., Gurnell, M., & Rustichini, A. (2009). Second-to-fourth digit ratio predicts success among high-frequency financial traders. *Proceedings of the National Academy of Sciences*, 106 (2), 623–628. https://doi.org/10.1073/pnas.0810907106
- Coates, J. M., Gurnell, M., & Sarnyai, Z. (2010). From molecule to market: Steroid hormones and financial risk-taking. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 365(1538), 331–343. https://doi.org/10.1098/rstb.2009.0193
- Crosier, B. S., Webster, G. D., & Dillon, H. M. (2012). Wired to connect: Evolutionary psychology and social networks. *Review of General Psychology*, 16(2), 230–239. https://doi.org/10.1037/ a0027919
- Dabbs, J. M., Jr. (1993). Salivary testosterone measurements in behavioral studies. Annals of the New York Academy of Sciences, 694(1), 177–183. https://doi.org/10.1111/j.1749-6632.1993. tb18351.x
- Dabbs, J. M., Jr., Carr, T. S., Frady, R. L., & Riad, J. K. (1995). Testosterone, crime, and misbehavior among 692 male prison inmates. *Personality and Individual Differences*, 18(5), 627–633. https://doi.org/10.1016/0191-8869(94)00177-T
- Dabbs, J. M., Jr., Frady, R. L., Carr, T. S., & Besch, N. F. (1987). Saliva testosterone and criminal violence in young adult prison inmates. *Psychosomatic Medicine*, 49(2), 174–182. https://doi. org/10.1097/00006842-198703000-00007
- Dabbs, J. M., Jr., & Hargrove, M. F. (1997). Age, testosterone, and behavior among female prison inmates. *Psychosomatic Medicine*, 59(5), 477.

- Davis, M., & Emory, E. (1995). Sex differences in neonatal stress reactivity. *Child Development*, 66 (1), 14–27. https://doi.org/10.1111/j.1467-8624.1995.tb00852.x
- Del Giudice, M., Ellis, B. J., & Shirtcliff, E. A. (2011). The adaptive calibration model of stress responsivity. *Neuroscience and Biobehavioral Reviews*, 35, 1562–1592. https://doi.org/10. 1016/j.neubiorev.2010.11.007
- Denson, T. F., Spanovich, M., & Miller, N. (2009). Cognitive appraisals and emotions predict cortisol and immune responses: A meta-analysis of acute laboratory social stressors and emotion inductions. *Psychological Bulletin*, 135, 823–853. https://doi.org/10.1037/a0016909
- Dickerson, S. S. (2008). Emotional and physiological responses to social-evaluative threat. *Social and Personality Psychology Compass*, 2(3), 1362–1378. https://doi.org/10.1111/j.1751-9004. 2008.00095.x
- Dickerson, S. S., & Kemeny, M. E. (2004). Acute stressors and cortisol responses: A theoretical integration and synthesis of laboratory research. *Psychological Bulletin*, 130(3), 355–391. https://doi.org/10.1037/0033-2909.130.3.355
- Dickerson, S. S., & Zoccola, P. M. (2013). Cortisol responses to social exclusion. In C. N. DeWall (Ed.), *The Oxford handbook of social exclusion* (pp. 143–151). Oxford, UK: Oxford University Press.
- Doane, L. D., & Adam, E. K. (2010). Loneliness and cortisol: Momentary, day-to-day, and trait associations. *Psychoneuroendocrinology*, 35(3), 430–441.
- Dreher, J.-C., Dunne, S., Pazderska, A., Frodl, T., Nolan, J. J., & O'Doherty, J. P. (2016). Testosterone causes both prosocial and antisocial status-enhancing behaviors in human males. *Proceedings of the National Academy of Sciences*, 113(41), 11633–11638. https://doi.org/10. 1073/pnas.1608085113
- Edwards, D. A., Wetzel, K., & Wyner, D. R. (2006). Intercollegiate soccer: Saliva cortisol and testosterone are elevated during competition, and testosterone is related to status and social connectedness with teammates. *Physiology and Behavior*, 87(1), 135–143. https://doi.org/10. 1016/j.physbeh.2005.09.007
- Eisenegger, C., Haushofer, J., & Fehr, E. (2011). The role of testosterone in social interaction. *Trends in Cognitive Sciences*, 15(6), 263–271. https://doi.org/10.1016/j.tics.2011.04.008
- Eisenegger, C., Naef, M., Snozzi, R., Heinrichs, M., & Fehr, E. (2010). Prejudice and truth about the effect of testosterone on human bargaining behaviour. *Nature*, 463(7279), 356–359. https:// doi.org/10.1038/nature08711
- Elias, M. (1981). Serum cortisol, testosterone, and testosterone-binding globulin responses to competitive fighting in human males. *Aggressive Behavior*, 7(3), 215–224.
- Feldman, R. (2015). The neurobiology of mammalian parenting and the biosocial context of human caregiving. *Hormones and Behavior*, 77, 3–17. https://doi.org/10.1016/j.yhbeh.2015.10.001
- Flinn, M. V., Ponzi, D., & Muehlenbein, M. P. (2012). Hormonal mechanisms for regulation of aggression in human coalitions. *Human Nature*, 23(1), 68–88. https://doi.org/10.1007/s12110-012-9135-y
- Folstad, I., & Karter, A. J. (1992). Parasites, bright males, and the immunocompetence handicap. *American Naturalist*, 139, 603–622.
- Ford, C. S., & Beach, F. A. (1951). *Patterns of sexual behavior*. Oxford: Harper and Paul B. Hoeber.
- Fuchs, E., Kirschbaum, C., Benisch, D., & Bieser, A. (1997). Salivary cortisol: A non-invasive measure of hypothalamo-pituitary-adrenocortical activity in the squirrel monkey, Saimiri sciureus. *Laboratory Animals*, 31(4), 306–311. https://doi.org/10.1258/002367797780596077
- Fuxjager, M. J., Mast, G., Becker, E. A., & Marler, C. A. (2009). The 'home advantage' is necessary for a full winner effect and changes in post-encounter testosterone. *Hormones and Behavior*, 56(2), 214–219. https://doi.org/10.1016/j.yhbeh.2009.04.009
- Garfield, Z. H., & Hagen, E. H. (in press). Investigating evolutionary models of leadership among recently settled Ethiopian hunter-gatherers. *The Leadership Quarterly*. https://doi.org/10. 1016/j.leaqua.2019.03.005

- Geniole, S. N., Bird, B. M., Ruddick, E. L., & Carré, J. M. (2017). Effects of competition outcome on testosterone concentrations in humans: An updated meta-analysis. *Hormones and Behavior*, 92, 37–50. https://doi.org/10.1016/j.yhbeh.2016.10.002
- Gladue, B. A., Boechler, M., & McCaul, K. D. (1989). Hormonal response to competition in human males. Aggressive Behavior, 15(6), 409–422.
- Glaser, R., Kiecolt-Glaser, J. K., Speicher, C. E., & Holliday, J. E. (1985). Stress, loneliness, and changes in herpesvirus latency. *Journal of Behavioral Medicine*, 8(3), 249–260.
- Granger, D. A., Fortunato, C. K., Beltzer, E. B., Virag, M., Bright, M., & Out, D. (2012). Salivary bioscience and research on adolescence: An integrated perspective. *Journal of Adolescence*, 32, 1081–1095. https://doi.org/10.1016/j.adolescence.2012.01.005
- Gray, P. B., McHale, T. S., & Carré, J. M. (2017). A review of human male field studies of hormones and behavioral reproductive effort. *Hormones and Behavior*, 91, 52–67. https://doi. org/10.1016/j.yhbeh.2016.07.004
- Gunnar, M. R., & Hostinar, C. E. (2015). The social buffering of the hypothalamic–pituitary– adrenocortical axis in humans: Developmental and experiential determinants. *Social Neurosci*ence, 10, 479–488. https://doi.org/10.1080/17470919.2015.1070747
- Gunnar, M. R., & Quevedo, K. (2007). The neurobiology of stress and development. Annual Review of Psychology, 58, 145–173. https://doi.org/10.1146/annurev.psych.58.110405.085605
- Gunnar, M. R., Sebanc, A. M., Tout, K., Donzella, B., & van Dulmen, M. M. H. (2003). Peer rejection, temperament, and cortisol activity in preschoolers. *Developmental Psychobiology*, 43, 346–368. https://doi.org/10.1002/dev.10144
- Ha, T., Rogers, A. A., Hibel, L. C., Saxbe, D. E., Laurent, H. K., & Granger, D. A. (2018). *Interpersonal attunement in the activity of the HPA axis: A review and meta-analysis.* Poster presented at the ISPNE Conference, Newport Beach, CA.
- Hackman, D. A., O'Brien, J. R., & Zalewski, M. (2018). Enduring association between parenting and cortisol: A Meta-analysis. *Child Development*, 89(5), 1485–1503.
- Harding, C. F. (1981). Social modulation of circulating hormone levels in the male. *Integrative and Comparative Biology*, 21(1), 223–231. https://doi.org/10.1093/icb/21.1.223
- Henrich, J. (2016). The secret of our success: How culture is driving human evolution, domesticating our species, and making us smarter. Princeton, NJ: Princeton University Press.
- Henrich, J., Chudek, M., & Boyd, R. (2015). The Big Man Mechanism: How prestige fosters cooperation and creates prosocial leaders. *Philosophical Transactions of The Royal Society B Biological Sciences*, 370(1683), 20150013. https://doi.org/10.1098/rstb.2015.0013
- Henrich, J., & Gil-White, F. J. (2001). The evolution of prestige: Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior*, 22(3), 165–196. https://doi.org/10.1016/S1090-5138(00)00071-4
- Henrich, J., Heine, S. J., & Norenzayan, A. (2010). The weirdest people in the world? *Behavioral and Brain Sciences*, 33(2–3), 61–83. https://doi.org/10.1017/S0140525X0999152X
- Hermans, E. J., Putman, P., Baas, J. M., Gecks, N. M., Kenemans, J. L., & van Honk, J. (2007). Exogenous testosterone attenuates the integrated central stress response in healthy young women. *Psychoneuroendocrinology*, 32(8–10), 1052–1061. https://doi.org/10.1016/j. psyneuen.2007.08.006
- Hermans, E. J., Putman, P., Baas, J. M., Koppeschaar, H. P., & Honk, J. v. (2006). A single administration of testosterone reduces fear-potentiated startle in humans. *Biological Psychiatry*, 59(9), 872–874. https://doi.org/10.1016/j.biopsych.2005.11.015
- Hinde, R. A. (1974). Biological bases of human social behaviour. New York, NY: McGraw-Hill.
- Hirschenhauser, K., & Oliveira, R. F. (2006). Social modulation of androgens in male vertebrates: Meta-analyses of the challenge hypothesis. *Animal Behaviour*, 71(2), 265–277. https://doi.org/ 10.1016/j.anbehav.2005.04.014
- Hostinar, C. E., Johnson, A. E., & Gunnar, M. R. (2015). Parent support is less effective in buffering cortisol stress reactivity for adolescents compared to children. *Developmental Science*, 18, 281–297. https://doi.org/10.1111/desc.12195

- Hostinar, C. E., Sullivan, R. M., & Gunnar, M. R. (2014). Psychobiological mechanisms underlying the social buffering of the hypothalamic–pituitary–adrenocortical axis: A review of animal models and human studies across development. *Psychological Bulletin*, 140, 256–282. https:// doi.org/10.1037/a0032671
- Jaeggi, A. V., Trumble, B. C., Kaplan, H. S., & Gurven, M. (2015). Salivary oxytocin increases concurrently with testosterone and time away from home among returning Tsimane' hunters. *Biology Letters*, 11(3), 20150058. https://doi.org/10.1098/rsbl.2015.0058
- Johnson, D. D. P., McDermott, R., Barrett, E. S., Cowden, J., Wrangham, R., McIntyre, M. H., & Rosen, S. P. (2006). Overconfidence in wargames: Experimental evidence on expectations, aggression, gender and testosterone. *Proceedings of the Royal Society B: Biological Sciences*, 273(1600), 2513–2520.
- Josephs, R. A., Newman, M. L., Brown, R. P., & Beer, J. M. (2003). Status, testosterone, and human intellectual performance: Stereotype threat as status concern. *Psychological Science*, 14 (2), 158–163. https://doi.org/10.1111/1467-9280.t01-1-01435
- Josephs, R. A., Sellers, J. G., Newman, M. L., & Mehta, P. H. (2006). The mismatch effect: When testosterone and status are at odds. *Journal of Personality and Social Psychology*, 90(6), 999–1013. https://doi.org/10.1037/0022-3514.90.6.999
- Kadushin, C. (2012). Understanding Social Networks. New York, NY: Oxford University Press.
- Kagan, J., Reznick, J. S., & Snidman, N. (1987). The physiology and psychology of behavioral inhibition in children. *Child Development*, 58(6), 1459–1473.
- Kemeny, M. E. (2003). The psychobiology of stress. Current Directions in Psychological Science, 12(4), 124–129.
- Kiecolt-Glaser, J. K., & Newton, T. L. (2001). Marriage and health: His and hers. *Psychological Bulletin*, 127, 472–503. https://doi.org/10.1037/0033-2909.127.4.472
- Knight, E. L., & Mehta, P. H. (2014). Hormones and hierarchies. In J. T. Cheng, J. L. Tracy, & C. Anderson (Eds.), *The psychology of social status* (pp. 269–301). New York, NY: Springer. https://doi.org/10.1007/978-1-4939-0867-7\_13
- Koolhaas, J., & Bohus, B. (1989). Social control in relation to neuroendocrine and immunological responses. In A. Steptoe & A. Appels (Eds.), *Stress, personal control and health* (pp. 295–305). Chichester: Wiley.
- Kornienko, O., Clemans, K., Out, D., & Granger, D. A. (2013). Friendship network position and salivary cortisol levels. *Social Neuroscience*, 8, 385–396. https://doi.org/10.1080/17470919. 2013.795500
- Kornienko, O., Clemans, K. H., Out, D., & Granger, D. A. (2014). Hormones, behavior, and social network analysis: Exploring associations between cortisol, testosterone, and network structure. *Hormones and Behavior*, 66, 534–544. https://doi.org/10.1016/j.yhbeh.2014.07.009
- Kornienko, O., Schaefer, D. R., Weren, S., Hill, G. W., & Granger, D. A. (2016). Cortisol and testosterone associations with social network dynamics. *Hormones and Behavior*, 80, 92–102. https://doi.org/10.1016/j.yhbeh.2016.01.013
- Kudielka, B. M., & Kirschbaum, C. (2005). Sex differences in HPA axis responses to stress: A review. *Biological Psychology*, 69(1), 113–132. https://doi.org/10.1016/j.biopsycho.2004.11. 009
- Kutsukake, N., Ikeda, K., Honma, S., Teramoto, M., Mori, Y., Hayasaka, I., ... Hasegawa, T. (2009). Validation of salivary cortisol and testosterone assays in chimpanzees by liquid chromatography-tandem mass spectrometry. *American Journal of Primatology*, 71(8), 696–706. https://doi.org/10.1002/ajp.20708
- Lazarus, R. S., & Folkman, S. (1984). Coping and adaptation. In W. D. Gentry (Ed.), *The handbook of behavioral medicine* (pp. 282–325). New York: Guilford.
- Lincoln, G. A., Guinness, F., & Short, R. V. (1972). The way in which testosterone controls the social and sexual behavior of the red deer stag (Cervus elaphus). *Hormones and Behavior*, 3(4), 375–396. https://doi.org/10.1016/0018-506X(72)90027-X

- Longman, D. P., Surbey, M. K., Stock, J. T., & Wells, J. C. K. (2018). Tandem androgenic and psychological shifts in male reproductive effort following a manipulated "win" or "loss" in a sporting competition. *Human Nature*, 29, 1–28. https://doi.org/10.1007/s12110-018-9323-5
- Loren Buck, C., & Barnes, B. M. (2003). Androgen in free-living arctic ground squirrels: Seasonal changes and influence of staged male-male aggressive encounters. *Hormones and Behavior*, 43 (2), 318–326. https://doi.org/10.1016/S0018-506X(02)00050-8
- Lutz, C. K., Tiefenbacher, S., Jorgensen, M. J., Meyer, J. S., & Novak, M. A. (2000). Techniques for collecting saliva from awake, unrestrained, adult monkeys for cortisol assay. *American Journal of Primatology*, 52(2), 93–99. https://doi.org/10.1002/1098-2345(200010)52:2<93:: AID-AJP3>3.0.CO;2-B
- Lynn, S. E. (2016). Endocrine and neuroendocrine regulation of fathering behavior in birds. *Hormones and Behavior*, 77, 237–248. https://doi.org/10.1016/j.yhbeh.2015.04.005
- Maner, J. K. (2017). Dominance and prestige: A tale of two hierarchies. Current Directions in Psychological Science, 26(6), 526–531. https://doi.org/10.1177/0963721417714323
- Maner, J. K., & Mead, N. L. (2010). The essential tension between leadership and power: When leaders sacrifice group goals for the sake of self-interest. *Journal of Personality and Social Psychology*, 99(3), 482–497. https://doi.org/10.1037/a0018559
- Mazur, A., & Booth, A. (1998). Testosterone and dominance in men. Behavioral and Brain Sciences, 21(03), 353–363.
- Mazur, A., Booth, A., & Dabbs, J. M., Jr. (1992). Testosterone and chess competition. Social Psychology Quarterly, 55(1), 70–77. https://doi.org/10.2307/2786687
- Mazur, A., & Lamb, T. A. (1980). Testosterone, status, and mood in human males. *Hormones and Behavior*, 14(3), 236–246. https://doi.org/10.1016/0018-506X(80)90032-X
- Mazur, A., Susman, E. J., & Edelbrock, S. (1997). Sex difference in testosterone response to a video game contest. *Evolution and Human Behavior*, 18(5), 317–326. https://doi.org/10.1016/S1090-5138(97)00013-5
- McCaul, K. D., Gladue, B. A., & Joppa, M. (1992). Winning, losing, mood, and testosterone. *Hormones and Behavior*, 26(4), 486–504. https://doi.org/10.1016/0018-506X(92)90016-O
- McEwen, B. S., & Gianaros, P. J. (2010). Central role of the brain in stress and adaptation: Links to socioeconomic status, health, and disease. *Annals of the New York Academy of Sciences*, 1186, 190–222. https://doi.org/10.1111/j.1749-6632.2009.05331.x
- Mead, N. L., & Maner, J. K. (2012). On keeping your enemies close: Powerful leaders seek proximity to ingroup power threats. *Journal of Personality and Social Psychology*, 102(3), 576–591. https://doi.org/10.1037/a0025755
- Mehta, P. H., & Josephs, R. A. (2006). Testosterone change after losing predicts the decision to compete again. *Hormones and Behavior*, 50(5), 684–692. https://doi.org/10.1016/j.yhbeh.2006. 07.001
- Mehta, P. H., Jones, A. C., & Josephs, R. A. (2008). The social endocrinology of dominance: Basal testosterone predicts cortisol changes and behavior following victory and defeat. *Journal of Personality and Social Psychology*, 94(6), 1078–1093. https://doi.org/10.1037/0022-3514.94.6. 1078
- Mehta, P. H., & Josephs, R. A. (2010). Testosterone and cortisol jointly regulate dominance: Evidence for a dual-hormone hypothesis. *Hormones and Behavior*, 58(5), 898–906.
- Mehta, P. H., Lawless DesJardins, N. M., van Vugt, M., & Josephs, R. A. (2017). Hormonal underpinnings of status conflict: Testosterone and cortisol are related to decisions and satisfaction in the hawk-dove game. *Hormones and Behavior*, 92, 141–154. https://doi.org/10.1016/j. yhbeh.2017.03.009
- Muller, M. N., Marlowe, F. W., Bugumba, R., & Ellison, P. T. (2009). Testosterone and paternal care in East African foragers and pastoralists. *Proceedings of the Royal Society of London B: Biological Sciences*, 276(1655), 347–354. https://doi.org/10.1098/rspb.2008.1028
- Muller, M. N., & Wrangham, R. W. (2004). Dominance, aggression and testosterone in wild chimpanzees: A test of the 'challenge hypothesis'. *Animal Behaviour*, 67(1), 113–123. https:// doi.org/10.1016/j.anbehav.2003.03.013

- Nave, G., Nadler, A., Dubois, D., Zava, D., Camerer, C., & Plassmann, H. (2018). Single-dose testosterone administration increases men's preference for status goods. *Nature Communications*, 9(1), 2433. https://doi.org/10.1038/s41467-018-04923-0
- Nave, G., Nadler, A., Zava, D., & Camerer, C. (2017). Single-dose testosterone administration impairs cognitive reflection in men. *Psychological Science*, 28(10), 1398–1407. https://doi.org/ 10.1177/0956797617709592
- Neave, N., & Wolfson, S. (2003). Testosterone, territoriality, and the 'home advantage'. *Physiology and Behavior*, 78(2), 269–275. https://doi.org/10.1016/S0031-9384(02)00969-1
- Nelson, R. J., & Trainor, B. C. (2007). Neural mechanisms of aggression. Nature Reviews Neuroscience, 8(7), 536–546. https://doi.org/10.1038/nrn2174
- Newman, M. L., Sellers, J. G., & Josephs, R. A. (2005). Testosterone, cognition, and social status. *Hormones and Behavior*, 47(2), 205–211. https://doi.org/10.1016/j.yhbeh.2004.09.008
- Newsom, J. T., Mahan, T. L., Rook, K. S., & Krause, N. (2008). Stable negative social exchanges and health. *Health Psychology*, 27(1), 78.
- Novak, M. A., Hamel, A. F., Kelly, B. J., Dettmer, A. M., & Meyer, J. S. (2013). Stress, the HPA axis, and nonhuman primate well-being: A review. *Applied Animal Behaviour Science*, 143(2), 135–149. https://doi.org/10.1016/j.applanim.2012.10.012
- O'Mailey, A. J., & Marsden, P. V. (2008). The analysis of social networks. *Health Services and Outcomes Research Methodology*, 8, 222–269. https://doi.org/10.1007/s10742-008-0041-z.
- Ohl, F., Kirschbaum, C., & Fuchs, E. (1999). Evaluation of hypothalamo-pituitary-adrenal activity in the tree shrew (Tupaia belangeri) via salivary cortisol measurement. *Laboratory Animals*, 33 (3), 269–274. https://doi.org/10.1258/002367799780578237
- Oliveira, R. F. (2004). Social modulation of androgens in vertebrates: Mechanisms and function. *Advances in the Study of Behavior*, *34*, 165–239.
- Oliveira, R. F., Lopes, M., Carneiro, L. A., & Canário, A. V. M. (2001). Watching fights raises fish hormone levels. *Nature*, 409(6819), 475–475. https://doi.org/10.1038/35054128
- Oxford, J., Ponzi, D., & Geary, D. C. (2010). Hormonal responses differ when playing violent video games against an ingroup and outgroup. *Evolution and Human Behavior*, 31(3), 201–209. https://doi.org/10.1016/j.evolhumbehav.2009.07.002
- Persky, H., Smith, K. D., & Basu, G. K. (1971). Relation of psychologic measures of aggression and hostility to testosterone production in man. *Psychosomatic Medicine*, 33(3), 265–277. https://doi.org/10.1097/00006842-197105000-00007
- Peters, E., Riksen-Walraven, J. M., Cillessen, A. H., & de Weerth, C. (2011). Peer rejection and HPA activity in middle childhood: Friendship makes a difference. *Child Development*, 82, 1906–1920.
- Pinter-Wollman, N., Hobson, E. A., Smith, J. E., Edelman, A. J., Shizuka, D., de Silva, S., ... McDonald, D. (2014). The dynamics of animal social networks: Analytical, conceptual, and theoretical advances. *Behavioral Ecology*, 25, 242–255. https://doi.org/10.1093/beheco/art047
- Ponzi, D., Zilioli, S., Mehta, P. H., Maslov, A., & Watson, N. V. (2016). Social network centrality and hormones: The interaction of testosterone and cortisol. *Psychoneuroendocrinology*, 68, 6–13. https://doi.org/10.1016/j.psyneuen.2016.02.014
- Pressman, S. D., Cohen, S., Miller, G. E., Barkin, A., Rabin, B. S., & Treanor, J. (2005). Loneliness, social network size, and immune response to influenza vaccination in college freshmen. *Health Psychology*, 24, 297–306. https://doi.org/10.1037/0278-6133.24.3.297
- Rankin, A., Swearingen-Stanborough, C., Granger, D. A., & Byrd-Craven, J. (2018). The role of co-rumination and adrenocortical attunement in young women's close friendships. *Psychoneuroendocrinology*, 98, 61–66.
- Raulo, A., & Dantzer, B. (2018). Associations between glucocorticoids and sociality across a continuum of vertebrate social behavior. *Ecology and Evolution*, 8(15), 7697–7716.
- Redhead, D. J., Cheng, J. T., Driver, C., Foulsham, T., & O'Gorman, R. (2018). On the dynamics of social hierarchy: A longitudinal investigation of the rise and fall of prestige, dominance, and social rank in naturalistic task groups. *Evolution and Human Behavior*, 40, 222–234.

- Ronay, R., Tybur, J. M., van Huijstee, D., & Morssinkhof, M. (2017). Embodied power, testosterone, and overconfidence as a causal pathway to risk-taking. *Comprehensive Results in Social Psychology*, 2(1), 28–43. https://doi.org/10.1080/23743603.2016.1248081
- Rook, K. S. (1984). The negative side of social interaction: Impact on psychological well-being. Journal of Personality and Social Psychology, 46(5), 1097.
- Rook, K. S. (2001). Emotional health and positive versus negative social exchanges: A daily diary analysis. *Applied Developmental Science*, 5(2), 86–97.
- Rose, R. M., Holaday, J. W., & Bernstein, I. S. (1971). Plasma testosterone, dominance rank and aggressive behaviour in male rhesus monkeys. *Nature*, 231(5302), 366–368. https://doi.org/10. 1038/231366a0
- Salvador, A., & Costa, R. (2009). Coping with competition: Neuroendocrine responses and cognitive variables. *Neuroscience and Biobehavioral Reviews*, 33(2), 160–170.
- Salvador, A., Suay, F., González-Bono, E., & Serrano, M. A. (2003). Anticipatory cortisol, testosterone and psychological responses to judo competition in young men. *Psychoneuroendocrinology*, 28(3), 364–375. https://doi.org/10.1016/S0306-4530(02)00028-8
- Salvador, A., Suay, F., Martinez-Sanchis, S., Simon, V. M., & Brain, P. F. (1999). Correlating testosterone and fighting in male participants in judo contests. *Physiology and Behavior*, 68 (1–2), 205–209. https://doi.org/10.1016/S0031-9384(99)00168-7
- Sapienza, P., Zingales, L., & Maestripieri, D. (2009). Gender differences in financial risk aversion and career choices are affected by testosterone. *Proceedings of the National Academy of Sciences*, 106(36), 15268–15273. https://doi.org/10.1073/pnas.0907352106
- Sapolsky, R. M. (2005). The influence of social hierarchy on primate health. Science, 308(5722), 648–652. https://doi.org/10.1126/science.1106477
- Sapolsky, R. M., Romero, L. M., & Munck, A. U. (2000). How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocrine Reviews*, 21(1), 55–89. https://doi.org/10.1210/edrv.21.1.0389
- Saxbe, D. E. (2008). A field (researcher's) guide to cortisol: Tracking HPA axis functioning in everyday life. *Health Psychology Review*, 2(2), 163–190. https://doi.org/10.1080/ 17437190802530812
- Schoofs, D., & Wolf, O. T. (2011). Are salivary gonadal steroid concentrations influenced by acute psychosocial stress? A study using the Trier Social Stress Test (TSST). *International Journal of Psychophysiology*, 80(1), 36–43. https://doi.org/10.1016/j.ijpsycho.2011.01.008
- Schultheiss, O. C., Wirth, M. M., & Stanton, S. J. (2004). Effects of affiliation and power motivation arousal on salivary progesterone and testosterone. *Hormones and Behavior*, 46(5), 592–599. https://doi.org/10.1016/j.yhbeh.2004.07.005
- Schultheiss, O. C., Wirth, M. M., Torges, C. M., Pang, J. S., Villacorta, M. A., & Welsh, K. M. (2005). Effects of implicit power motivation on men's and women's implicit learning and testosterone changes after social victory or defeat. *Journal of Personality and Social Psychol*ogy, 88(1), 174–188. https://doi.org/10.1037/0022-3514.88.1.174
- Setchell, J. M., & Dixson, A. F. (2001). Changes in the secondary sexual adornments of male Mandrills (Mandrillus sphinx) are associated with gain and loss of alpha status. *Hormones and Behavior*, 39(3), 177–184. https://doi.org/10.1006/hbeh.2000.1628
- Sethre-Hofstad, L., Stansbury, K., & Rice, M. A. (2002). Attunement of maternal and child adrenocortical response to child challenge. *Psychoneuroendocrinology*, 27(6), 731–747.
- Seyfarth, R. M., & Cheney, D. L. (2013). Affiliation, empathy, and the origins of theory of mind. Proceedings of the National Academy of Sciences, 110(Supplement 2), 10349–10356.
- Shoal, G. D., Giancola, P. R., & Kirillova, G. P. (2003). Salivary cortisol, personality, and aggressive behavior in adolescent boys: A 5-year longitudinal study. *Journal of the American Academy of Child and Adolescent Psychiatry*, 42(9), 1101–1107.
- Silk, J. B. (2007). Social components of fitness in primate groups. Science, 317, 1347–1351.
- Slatcher, R. B., Mehta, P. H., & Josephs, R. A. (2011). Testosterone and self-reported dominance interact to influence human mating behavior. *Social Psychological and Personality Science*, 2 (5), 531–539. https://doi.org/10.1177/1948550611400099

- Smider, N. A., Essex, M. J., Kalin, N. H., Buss, K. A., Klein, M. H., Davidson, R. J., & Goldsmith, H. H. (2002). Salivary cortisol as a predictor of socioemotional adjustment during kindergarten: A prospective study. *Child Development*, 73(1), 75–92.
- Snijders, T. A. B. (2011). Statistical models for social networks. Annual Review of Sociology, 37, 131–153. https://doi.org/10.1146/annurev.soc.012809.102709
- Snyder, J. K., Kirkpatrick, L. A., & Barrett, H. C. (2008). The dominance dilemma: Do women really prefer dominant mates? *Personal Relationships*, 15(4), 425–444.
- Stanton, S. J., Beehner, J. C., Saini, E. K., Kuhn, C. M., & LaBar, K. S. (2009). Dominance, politics, and physiology: Voters' testosterone changes on the night of the 2008 United States presidential election. *PLoS One*, 4(10), e7543. https://doi.org/10.1371/journal.pone.0007543
- Stanton, S. J., & Schultheiss, O. C. (2009). The hormonal correlates of implicit power motivation. Journal of Research in Personality, 43(5), 942–949. https://doi.org/10.1016/j.jrp.2009.04.001
- Steptoe, A., Owen, N., Kunz-Ebrecht, S. R., & Brydon, L. (2004). Loneliness and neuroendocrine, cardiovascular, and inflammatory stress responses in middle-aged men and women. *Psychoneuroendocrinology*, 29, 593–611. https://doi.org/10.1016/S0306-4530(03)00086-6
- Tamres, L. K., Janicki, D., & Helgeson, V. S. (2002). Sex differences in coping behavior: A metaanalytic review and an examination of relative coping. *Personality and Social Psychology Review*, 6(1), 2–30.
- Taylor, S. E. (2006). Tend and befriend biobehavioral bases of affiliation under stress. *Current Directions in Psychological Science*, 15, 273–277.
- Taylor, S. E. (2011). Tend and befriend theory. In P. A. M. Van Lange, A. W. Kruglanski, & E. T. Higgins (Eds.), *Handbook of theories of social psychology: Collection* (Vol. 1 & 2, p. 32). Thousand Oaks, CA: Sage.
- Taylor, S. E., Klein, L. C., Lewis, B. P., Gruenewald, T. L., Gurung, R. A., & Updegraff, J. A. (2000). Biobehavioral responses to stress in females: Tend-and-befriend, not fight-or-flight. *Psychological Review*, 107(3), 411.
- Timmons, A. C., Margolin, G., & Saxbe, D. E. (2015). Physiological linkage in couples and its implications for individual and interpersonal functioning: A literature review. *Journal of Family Psychology*, 29(5), 720–731.
- Trumble, B. C., Cummings, D., von Rueden, C., O'Connor, K. A., Smith, E. A., Gurven, M., & Kaplan, H. (2012). Physical competition increases testosterone among Amazonian foragerhorticulturalists: A test of the 'challenge hypothesis'. *Proceedings of the Royal Society of London B: Biological Sciences*, 279(1739), 2907–2912. https://doi.org/10.1098/rspb.2012.0455
- Trumble, B. C., Smith, E. A., O'Connor, K. A., Kaplan, H. S., & Gurven, M. D. (2014). Successful hunting increases testosterone and cortisol in a subsistence population. *Proceedings of the Royal Society of London B: Biological Sciences*, 281(1776), 20132876. https://doi.org/10.1098/rspb. 2013.2876
- Tsigos, C., & Chrousos, G. P. (2002). Hypothalamic–pituitary–adrenal axis, neuroendocrine factors and stress. *Journal of Psychosomatic Research*, 53(4), 865–871. https://doi.org/10.1016/S0022-3999(02)00429-4
- Valtorta, N. K., Kanaan, M., Gilbody, S., Ronzi, S., & Hanratty, B. (2016). Loneliness and social isolation as risk factors for coronary heart disease and stroke: Systematic review and metaanalysis of longitudinal observational studies. *Heart*, 102(13), 1009–1016.
- van Anders, S. M., & Watson, N. V. (2006). Social neuroendocrinology: Effects of social contexts and behaviors on sex steroids in humans. *Human Nature*, 17(2), 212–237. https://doi.org/10. 1007/s12110-006-1018-7
- van Honk, J., & Schutter, D. J. L. G. (2007). Testosterone reduces conscious detection of signals serving social correction: Implications for antisocial behavior. *Psychological Science*, 18(8), 663–667. https://doi.org/10.1111/j.1467-9280.2007.01955.x
- van Honk, J., Tuiten, A., Verbaten, R., van den Hout, M., Koppeschaar, H., Thijssen, J., & de Haan, E. (1999). Correlations among salivary testosterone, mood, and selective attention to threat in humans. *Hormones and Behavior*, 36(1), 17–24. https://doi.org/10.1006/hbeh.1999.1521

- van Honk, J., Will, G.-J., Terburg, D., Raub, W., Eisenegger, C., & Buskens, V. (2016). Effects of testosterone administration on strategic gambling in poker play. *Scientific Reports*, 6, 18096. https://doi.org/10.1038/srep18096
- Vleck, C. M., & Brown, J. L. (1999). Testosterone and social and reproductive behaviour in Aphelocoma jays. Animal Behaviour, 58(5), 943–951. https://doi.org/10.1006/anbe.1999.1226
- von Rueden, C., Gurven, M., & Kaplan, H. (2011). Why do men seek status? Fitness payoffs to dominance and prestige. *Proceedings of the Royal Society B: Biological Sciences*, 278(1715), 2223.
- Vongas, J. G., & Al Hajj, R. (2017). The effects of competition and implicit power motive on men's testosterone, emotion recognition, and aggression. *Hormones and Behavior*, 92, 57–71. https:// doi.org/10.1016/j.yhbeh.2017.04.005
- Walker, M. E., Wasserman, S., & Wellman, B. (1993). Statistical models for social support networks. Sociological Methods Research, 22, 71–98. https://doi.org/10.1177/ 0049124193022001004
- Wasserman, S., & Faust, K. (1994). Social network analysis: Methods and applications. Cambridge: Cambridge University Press.
- Weiner, H. (1992). *Perturbing the organism: The biology of stressful experience*. Chicago, IL: University of Chicago Press.
- Wingfield, J. C. (2017). The challenge hypothesis: Where it began and relevance to humans. *Hormones and Behavior*, 92, 9–12. https://doi.org/10.1016/j.yhbeh.2016.11.008
- Wingfield, J. C., Ball, G. F., Dufty, A. M., Hegner, R. E., & Ramenofsky, M. (1987). Testosterone and aggression in birds. *American Scientist*, 75(6), 602–608.
- Wingfield, J. C., Hegner, R. E., Dufty, A. M., & Ball, G. F. (1990). The "Challenge Hypothesis": Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *The American Naturalist*, 136(6), 829–846.
- Wingfield, J. C., Jacobs, J. D., Tramontin, A. D., Perfito, N., Meddle, S., Maney, D. L., & Soma, K. (2000). Toward an ecological basis of hormone–behavior interactions in reproduction of birds. In K. Wallen & J. E. Schneider (Eds.), *Reproduction in context. Social and environmental influences on reproduction* (pp. 85–128). Cambridge, MA: MIT Press.
- Wingfield, J. C., Lynn, S. E., & Soma, K. K. (2001). Avoiding the 'costs' of testosterone: Ecological bases of hormone-behavior interactions. *Brain, Behavior and Evolution*, 57(5), 239–251. https://doi.org/10.1159/000047243
- Worthman, C. M., & Konner, M. J. (1987). Testosterone levels change with subsistence hunting effort inU+202F.!Kung San Men. *Psychoneuroendocrinology*, 12(6), 449–458. https://doi.org/ 10.1016/0306-4530(87)90079-5
- Wrangham, R. W. (2018). Two types of aggression in human evolution. Proceedings of the National Academy of Sciences, 115(2), 245–253. https://doi.org/10.1073/pnas.1713611115
- Wu, Y., Eisenegger, C., Sivanathan, N., Crockett, M. J., & Clark, L. (2017). The role of social status and testosterone in human conspicuous consumption. *Scientific Reports*, 7(1), 11803. https:// doi.org/10.1038/s41598-017-12260-3
- Zethraeus, N., Kocoska-Maras, L., Ellingsen, T., von Schoultz, B., Hirschberg, A. L., & Johannesson, M. (2009). A randomized trial of the effect of estrogen and testosterone on economic behavior. *Proceedings of the National Academy of Sciences*, 106(16), 6535–6538. https://doi.org/10.1073/pnas.0812757106
- Zilioli, S., & Bird, B. M. (2017). Functional significance of men's testosterone reactivity to social stimuli. *Frontiers in Neuroendocrinology*, 47, 1–18. https://doi.org/10.1016/j.yfrne.2017.06. 002
- Zilioli, S., & Watson, N. V. (2012). The hidden dimensions of the competition effect: Basal cortisol and basal testosterone jointly predict changes in salivary testosterone after social victory in men. *Psychoneuroendocrinology*, 37(11), 1855–1865. https://doi.org/10.1016/j.psyneuen.2012.03. 022
- Zilioli, S., & Watson, N. V. (2014). Testosterone across successive competitions: Evidence for a 'winner effect' in humans? *Psychoneuroendocrinology*, 47, 1–9. https://doi.org/10.1016/j. psyneuen.2014.05.001