

Hormonal Mechanisms for Regulation of Aggression in Human Coalitions

Mark V. Flinn · Davide Ponzi ·
Michael P. Muehlenbein

Published online: 14 March 2012
© Springer Science+Business Media, LLC 2012

Abstract Coalitions and alliances are core aspects of human behavior. All societies recognize alliances among communities, usually based in part on kinship and marriage. Aggression between groups is ubiquitous, often deadly, fueled by revenge, and can have devastating effects on general human welfare. Given its significance, it is surprising how little we know about the neurobiological and hormonal mechanisms that underpin human coalitionary behavior. Here we first briefly review a model of human coalitionary behavior based on a process of runaway social selection. We then present several exploratory analyses of neuroendocrine responses to coalitionary social events in a rural Dominican community, with the objective of understanding differences between in-group and out-group competition in adult and adolescent males. Our analyses indicate: (1) adult and adolescent males do not elevate testosterone when they defeat their friends, but they do elevate testosterone when they defeat outsiders; (2) pre-competition testosterone and cortisol levels are negatively associated with strength of coalitionary ties; and (3) adult males usually elevate testosterone when interacting with adult women who are potential mates, but in a striking reversal, they have lower testosterone if the woman is a conjugal partner of a close friend. These naturalistic studies hint that reciprocity, dampening of aggression, and competition among friends and allies may be biologically embedded in unique ways among humans.

M. V. Flinn (✉)
Department of Anthropology, University of Missouri, 107 Swallow Hall, Columbia, MO 65211, USA
e-mail: FlinnM@missouri.edu

D. Ponzi
Division of Biological Sciences, University of Missouri, Columbia, MO, USA

M. P. Muehlenbein
Department of Anthropology, Indiana University, Bloomington, IN, USA

Keywords Coalitions · Aggression · Human biology · Evolution · Hormone · Testosterone · Neuroendocrine · Cooperation

Once alliances start to form, there is no other reasonable strategy but to join one (Gavrilets et al. 2008:44).

No hunt needs quite so much forethought or ability to communicate complex instructions as does a war, nor do such drastic demographic consequences hinge on the outcome (Hamilton 1975:344).

Coalitions and alliances are core aspects of human sociality. Humans cooperate in a broad range of activities, including aggression and defense against other groups of humans (Carneiro 1970; Chagnon 1968, 1979a, 2012; Harcourt and de Waal 1992; Tiger 1969; Tiger and Fox 1971; Wrangham 1999). Mortality rates from intergroup conflicts in tribal societies for adult males average 10% to 30% (Beckerman et al. 2009; Chagnon et al. 1979; Ember and Ember 1997; Keeley 1996; Knauff 1991). Long-term planning for intergroup conflict and cycles of “blood revenge” are commonplace (Boehm 1984; Chagnon 1988; Gould 1999, 2000; Jacoby 1983; Otterbein 1994). Conflict among human ancestors may have a deep evolutionary history (Walker 2001; Wu et al. 2011). Surprisingly, given the key role of coalitionary behavior in human affairs, and its unique complexities, we do not know much about the neurobiological and hormonal mechanisms that facilitate and constrain cooperative in-group and out-group relationships, nor how such mechanisms develop during childhood and adolescence.

Here we first review briefly a model for the evolution of human coalitionary behavior based on a process of runaway social selection (Alexander 1971, 1974, 1990, 2012; Flinn and Alexander 2007; Gavrilets et al. 2008; Nesse 2007). We then examine possible neuroendocrine mechanisms that underpin coalitionary relationships with several empirical examples from a longitudinal study of a horticultural community on the island of Dominica. Our goal is to contribute to a Tinbergen (1963) synthesis of neuroendocrine/cognitive mechanisms, ontogeny, phylogeny, and evolutionary function of human coalitionary behavior.

The Evolution of Human Coalitionary Behaviors

A hydrogen bomb is an example of mankind’s enormous capacity for friendly cooperation. Its construction requires an intricate network of human teams, all working with single-minded devotion toward a common goal. Let us pause and savor the glow of self-congratulation we deserve for belonging to such an intelligent and sociable species (Bigelow 1969:1).

Humans are highly prosocial; we are embedded in extensive networks of friends, family, neighbors, coworkers, acquaintances, and others (Binmore 2006; Boehm 1999; DeScioli and Kurzban 2009; Ridley 1996; Trivers 1971; Wright 1994). Empathy and morality are fundamental human traits (Alexander 1987; de Waal 2009; Fehr and Fischbacher 2003). Our treasured, seemingly benevolent

characteristics of kindness, generosity, honor, humility, and loyalty appear to have evolved, however, not as adaptations to extrinsic ecological pressures but arguably as a consequence of social dynamics generated by competition within and between groups (Alexander 1990, 2012; Bowles 2009; Choi and Bowles 2007; Flinn et al. 2005a; Frank 1995, 2003; Nesse 2007). The apparent primary purpose of human coalitions is to outcompete other human coalitions.

Evidence for the evolutionary trajectory of human family, kinship, and intergroup relations over the past one million years is indirect. We hypothesize that human cognition, extended families (with multiple generations), mating strategies, biparental care, and the capabilities for coalitionary relationships coevolved. Evidence in support of this hypothesis comes in part from (1) comparisons with extinct and extant hominoids and hunter-gatherer cultures and (2) complex neuroendocrine mechanisms that appear to mediate these unusual human traits.

Comparisons with Extinct and Extant Primates and Hunter-Gatherer Cultures

Some components of human and chimpanzee coalitionary psychology are more likely homoplasies (independently evolved) than synapomorphies (shared derived). Body-size sexual dimorphism is an unambiguous indicator of male-male competition associated with a polygynous mating system (Alexander et al. 1979; Plavcan and van Schaik 1997) as well as the absence of significant coalitionary behavior among males (Plavcan et al. 1995). And although others may disagree (Reno et al. 2003), some australopithecine and early *Homo* ancestors were likely more sexually dimorphic than either modern humans or chimpanzees (Frayer and Wolpoff 1985; McHenry 1992; Plavcan 2012; Plavcan et al. 2005). In addition, modern humans differ from other primate species (and likely the hominid ancestors) in the relative nature and degree of stable breeding bonds, male parental investment, extended bilateral kin networks, reciprocal exogamy, and concealed ovulation, all of which may have coevolved with abilities for humans to develop intensive coalitionary behaviors (Alexander 1990; Chapais 2008; Rodseth et al. 1991).

Although humans and chimpanzees may share some general cooperative behaviors (Warneken and Tomasello 2009), human coalitionary behaviors differ significantly from those of extant great apes (Manson and Wrangham 1991; Rodseth and Wrangham 2004). Chimpanzees, for example, rarely fight group against group: border patrols usually will attack solitary individuals or small groups, not large congregations (Wrangham 1999; also see Wrangham and Glowacki 2012). Great apes do not have alliances between communities to attack/defend themselves from other (third) groups, and they do not control mating/marriage relationships with consequences for relations between kin groups.

Great apes do not appear to have any cooperative relationships with individuals outside their own group, not even with their sisters or brothers living in neighboring communities. For example, chimpanzee (*Pan troglodytes*) communities have exclusive male patrilineal lines that have not been observed to fuse or mix with male patrilineal lines from other communities (Watts et al. 2006). Brothers often help brothers in the same community (Boehm 1992), but males do not appear to help their sisters in neighboring communities (and vice versa). Bonobos also lack the distinctive human networks of intercommunity alliances based on bilateral kinship and marriage. Male

chimpanzees and bonobos share a common diffuse parental interest in juveniles in their community because paternity is obscure. Human males, in contrast, have targeted interests in their families in part because paternity is relatively certain. Human communities must therefore overcome the consequent factions between families with cooperative interfamily relations. Humans, moreover, develop cooperative intercommunity linkages involving residential reciprocity (e.g., brideservice) and complex kin lineages (e.g., Chagnon 1979b; Walker et al. 2011).

The intermediate evolutionary steps between an animal with chimpanzee-, bonobo-, or gorilla-like social structure and humans are difficult to explain (Chapais 2008, 2010, 2011; Flinn 2011; Flinn et al. 2005a, 2007; Geary 2005, 2010; Geary and Flinn 2001, 2002; Rodseth et al. 1991). The evolution of paternal care is especially problematic. Mammals that live in groups with multiple males, such as bonobos, chimpanzees, dolphins, and squirrel monkeys, usually exhibit minimal paternal care owing to uncertain paternity (Alexander 1974; Clutton-Brock 1991; Conner et al. 2001). The formation of exclusive “pair-bonds” between males and females in multiple-male groups would provide cues of nonpaternity to other males, which could facilitate infanticide by them (Hrdy 1999; cf. Borries et al. 2011; Henzi et al. 2010). Chimpanzee males, for example, do not tolerate exclusive mating relationships by other males (e.g., Muller et al. 2011; cf. Watts 1998); neither do dolphins, whose alliances are in some respects even more complex than those of great apes (Conner 2010).

In contrast, exclusive mating relationships are common among humans and are linked to fathers providing protection, information, food, and social status for their children (Gray and Anderson 2010; Hewlett 1992; Lamb 2004; Storey et al. 2000). In this respect, humans seem more similar to gorillas (*Gorilla* spp.) and gibbons (Hylobatidae) than to dolphins, chimpanzees, or bonobos (Geary and Flinn 2001). Gorillas and gibbons, however, rarely tolerate other males’ mating relationships: gorilla silverbacks usually do not reside or cooperate with other silverbacks (Watts 1996), and adult male gibbons defend exclusive territories for their families against intrusions by outside males (Palombit 1994). These obstacles suggest that gorilla or gibbon models of early human family and coalitionary behaviors are unlikely.

If human ancestors had intergroup relations similar to those of chimpanzees (see Boesch et al. 2008; Mitani et al. 2010; Watts et al. 2006; Wrangham 1999; Wrangham and Peterson 1996), it would have been difficult to make even the first steps toward cooperative alliances among males (and females) in different communities. An adult male attempting to establish a relationship with another group would likely be killed. Somehow our ancestors overcame such initial obstacles to intercommunity alliances. It is possible that our ancestors did not have hostile intergroup relations; this seems unlikely, however, on both empirical (LeBlanc 2003) and theoretical (Alexander 1990, 2012; Gavrilets and Vose 2006; Gavrilets et al. 2008; Kurzban and Neuberg 2005; Nowak 2006; Shaller and Neuberg 2008; Stevens et al. 2005; van Vugt et al. 2007; Wrangham 1999) grounds.

Recognition of kinship among individuals residing in different communities is key to intergroup cooperation. Humans are different from other hominoids in the coevolutionary development of (a) stable and moderately exclusive breeding bonds, (b) bilateral kin recognition and relationships, (c) affinal ties, and (d) reciprocity among coresident and nonresident families (Alexander 1979, 1990; Chapais 2008, 2010,

2011; Flinn 2011; Flinn and Low 1986; Flinn et al. 2007; Hrdy 2009; Muehlenbein and Flinn 2011; Quinlan 2008). The extended human family appears to be a critical building block for the evolution of more complex communities, such as the patrilocality band (Chapais 2008) and the tribe (Rodseth and Wrangham 2004), with flexible residence choice with kin in multiple communities and apparent intentional cultivation of ties with relatives in multiple locations (e.g., Hughes 1988; Marlowe 2010; Walker et al. 2010; Wiessner 2002). The cognitive and neuroendocrine mechanisms that facilitate these distinctive human traits are incompletely understood.

Neuroendocrine Mechanisms of Coalitionary Behaviors

The neuroendocrine system is a complex set of mechanisms designed by natural selection to communicate information among cells and tissues. Steroid and peptide hormones, neurotransmitters, and other chemical messengers guide behaviors of mammals in many important ways (Ellison and Gray 2009; Henley et al. 2011; Lee et al. 2009; Ophir 2011; Ostner et al. 2011; Panksepp 2009; Young et al. 2011). An important challenge confronting human evolutionary biologists and psychologists is to understand how the neuroendocrine system has become linked with cognitive systems (e.g., Adolphs 2003a, b; Allman et al. 2011; Flinn et al. 2005b; Rilling and Sanfey 2011; Ulrich-Lai and Herman 2009) to produce the unique suite of human family and coalitionary behaviors.

Several hormones, most notably testosterone, oxytocin, and arginine vasopressin, are likely central to the development and maintenance of human male coalitions. Social effects such as victories against outsiders typically produce elevations in testosterone (Bernhardt et al. 1998; Fuxjager et al. 2009; Gleason et al. 2009; González-Bono et al. 1999; 2000; Oxford et al. 2010; Wagner et al. 2002). Like members of other taxa (Hirschenhauser and Oliveira 2006; Wingfield et al. 1990; Wobber et al. 2010), human males usually elevate testosterone in anticipation of one-on-one competitive events against other males (Gladue et al. 1989; Salvador 2005; Salvador and Costa 2009; Salvador et al. 1987). This may function to augment muscle tissue (especially upper-body strength), which itself may have been selected to facilitate the production and use of weapons to settle male-male conflicts (Bercovitch 2001). Elevated testosterone levels prior to competition may also improve coordination and cognitive performance, increase self-confidence and motivation, as well as possibly interfere with self-control (Salvador et al. 2003). The effects are not simply constrained to those directly competing, but also to those observing the competition (Bernhardt et al. 1998).

If a male is victorious in competition, his testosterone levels may increase, possibly to facilitate further successful competition in winners; if defeated, testosterone levels usually decrease, possibly to temper provocative actions of losers (Booth et al. 1989; Dabbs and Dabbs 2000; Flinn et al. 1998; González-Bono et al. 1999, 2000; Maner et al. 2008; Mazur et al. 1992; Schultheiss et al. 1999). Decreased testosterone levels would also function to prevent immunosuppression and other costs associated with otherwise elevated testosterone levels (Muehlenbein 2008; Muehlenbein et al. 2010). This would be particularly advantageous if the loser of the competition was injured.

The mechanisms by which testosterone levels change could involve acute alterations in gonadotropin-releasing hormone or luteinizing hormone, albumin or sex

hormone-binding globulin concentration (Trumble et al. 2011), tissue uptake of testosterone, conversion of hormones to or from testosterone (i.e., dehydroepiandrosterone to androstenedione to testosterone, or testosterone to estradiol), or clearance of hormones through the liver and kidneys. Two lines of evidence suggest the importance of disassociation/association between testosterone and carrier proteins or steroidogenic enzyme conversion. First, competition-associated changes in testosterone are also found in women (Bateup et al. 2002; Edwards et al. 2006; Edwards and Kurlander 2010; Kivlighan et al. 2005; Oliveira et al. 2009), suggesting that testes are not required for such changes. Second, it can take more than an hour for changes in luteinizing-hormone concentration to cause peak changes in gonadal production of testosterone in young men (Veldhuis and Iranmanesh 2004). Therefore, rapid changes in both men and women are likely the result of other mechanisms outside the hypothalamic-pituitary-gonadal axis.

Studies of testosterone response in industrialized societies have found that high levels of testosterone are associated with status seeking, antisocial behavior, and decreased generosity (Archer 2006; Zak et al. 2009), whereas low testosterone levels are often associated with affiliative behaviors. Low testosterone levels have been posited to be advantageous for group (rather than individual) competition because low testosterone could enhance cooperation among teammates by decreasing personal (selfish individual) dominance-seeking (Mehta et al. 2009). Given the importance of cooperative relationships within coalitions of humans, hormonal responses to competitive events may be contingent on whether members of the opposing team are in-group or out-group (Flinn et al. 1998; Oxford et al. 2010; Wagner et al. 2002).

Although some have suggested that the peptide hormone oxytocin underpins generalized prosocial behavior in humans (Domes et al. 2010; Kosfeld et al. 2005; Zak et al. 2005), others suggest that oxytocin motivates affiliative behavior toward specific in-group targets (de Dreu et al. 2010, 2011; Ditzen et al. 2009; Miller 2010; Shamay-Tsoory et al. 2009; Theodoridou et al. 2009) consistent with discriminative nepotism and reciprocity (Alexander 1991, 2006; Daly and Wilson 1995). Studies of effects of neurotransmitters (e.g., serotonin, dopamine) also suggest specific targeting rather than generalized altruism (Crockett 2009; Crockett et al. 2010; Tse and Bond 2002).

The biochemical mechanisms responsible for the regulation of bonds between mates, and between parents and offspring (Bartels and Zeki 2004; Bridges 2008; Carter 2002; Curtis and Wang 2003; Fisher 2002; Young and Insel 2002), also are likely involved in other types of intragroup bonding in humans. That is, the elevated arginine vasopressin, prolactin, and oxytocin that prepare males to be receptive to and care for infants (Bales et al. 2004) may be part of the neuroendocrine system that facilitates coalitionary relationships. The same might be said for the importance of the linkage between oxytocin and the dopamine D2 receptors in the nucleus accumbens responsible for positive reward in mental states (Aragona et al. 2003).

Analysis of patterns of hormone levels in naturalistic contexts can provide important insights into the evolutionary functions of the neuroendocrine mechanisms that guide human behaviors. Clinical and experimental studies may have novel or artificial conditions that potentially influence hormone responses. Naturalistic studies, on the other hand, usually cannot provide high levels of control and repeatability. In the following sections we present analyses of data on testosterone and cortisol responses

to coalitionary events from our long-term (1988 through 2011) study of a rural horticultural community on the east coast of Dominica (see Flinn 2006, 2009; Quinlan and Flinn 2005).¹ Our objective is to examine potential distinctive characteristics of human coalitionary behavior. We examine testosterone and cortisol responses to group competition as well as testosterone responses to potential mates. Given small sample sizes, the case examples in the following sections are intended as explorations of the diversity and nuance of hormonal responses to the complex challenges of human sociality. We challenge interested readers to comprehensively evaluate our hypotheses, and in particular to pursue research that includes measurements of oxytocin, arginine vasopressin, prolactin, and neurotransmitters, ideally in concert with information about binding at specific receptor sites.

The Dominoes Competition

If androgen response to competitive outcomes influences subsequent affiliation, then elevation of testosterone is expected among members of a team that is victorious over out-group teams, but not when they defeat in-group teams (those containing their coalition partners). We speculate that elevated levels of androgens may diminish psychological states that are conducive to reconciliation (de Waal 2000) between competitors, while at the same time enhancing bonds among victorious coalition members.

In the study community of Bwa Mawego, Dominica, domino is a commonplace competitive team sport. The game is played by four players organized in teams of two against two. Although dominoes usually involves more cognitive than physical effort, players often become quite animated and evidence intense social competition, accompanied by hormonal responses. Changes in testosterone levels in response to in- versus out-group competition in dominoes were assessed from saliva samples collected from 27 healthy adult men aged 25–52 (16 pairs; 5 men were in two events, but with different conditions for in-group/out-group or win/loss; the study includes 12 men sampled in 2000 from informal tournaments previously reported in Wagner et al. 2002, and 15 additional men sampled from unarranged events in 2001–2002) the morning of, immediately before, immediately after, and 30–60 min after the end of the competition.

All domino events occurred in the afternoon or early evening (14:00–19:00); there were no apparent effects of time of collection or age of player; analyses examine changes in levels of T for each individual in response to the competitive event. For all samples, sugarfree spearmint gum was used to stimulate saliva, which was collected in a 5 ml polypropylene centrifuge tube containing sodium azide. Free testosterone was quantified via a radioimmunoassay (Coat-a-Count, Diagnostic Product Corporation) according to the manufacturer's instructions. All individual samples were run in duplicate with standards and high and low concentration controls (controls within acceptable ranges). All samples were run in a single assay, and the intra-assay coefficient of variation was less than 5%.

Because of the small sample size and within-subject design, changes in testosterone levels across events (pre- and post-competition) were examined by means of

¹ Also see supporting materials accessible online at <http://web.missouri.edu/~flinnm/>.

nonparametric Friedman and Wilcoxon signed-rank tests using proc freq in SAS. Where the Friedman statistic was significant, multiple comparison analysis with relative pairwise adjustment was used, following Siegel and Castellan 1988 (Soliani 2008). Changes in testosterone levels across events (pre- and post-competition) were examined within individuals. Further, percent change in testosterone level across events (pre- and post-competition) were examined between winners and losers with the Wilcoxon sum rank test using proc npar1way in SAS.

Results reveal that winning against an out-group team (not containing one's coalitionary partners) was associated with an increase in testosterone at the end of the match compared with baseline ($Q=20.70$, $N=8$, $p<0.001$; Fig. 1a). For losers against out-group teams, testosterone levels were lower by 30–60 min post competition compared with pre-match levels ($Q=20.50$, $N=8$, $p<0.001$; Fig. 1b). While at the end of the out-group game there were no differences in testosterone percent change between losers and winners ($Z=1.31$, $p>0.05$; Fig. 2a), winners had significantly higher levels of T compared with pre-match levels than did losers 30–60 min post competition ($Z=3.30$, $p<0.01$; Fig. 2b).

When subjects competed against teams of friends in the same tournament, there were no significant changes in testosterone levels for winners or losers (Fig. 3a and b). In addition, there were no differences in percent change in testosterone between winners and losers during the in-group competition ($Z=0.47$, $p>0.10$ and $Z=-0.15$,

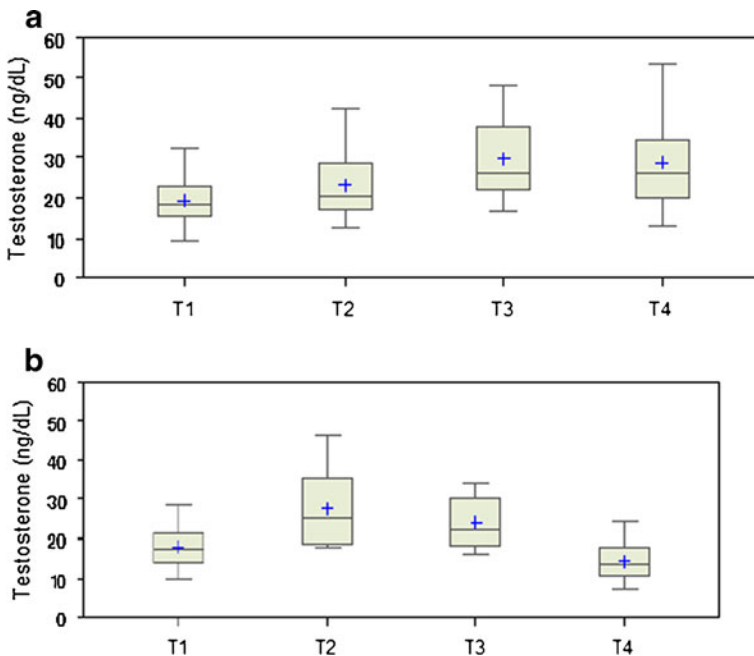


Fig. 1 **a** Testosterone levels when victorious over an out-group team. Winning against a group of outsiders increased testosterone levels at times 3 (T3) and 4 (T4) ($Q=20.70$, $N=8$, $p<0.001$). T1=baseline hours before competition; T2=at the beginning of the competition; T3=at the end of the competition; T4=30–60 min after the end of the competition. **b** Testosterone levels when defeated by an out-group team. Losing to a group of outsiders was associated with lowered testosterone levels immediately after and 30–60 min after competition compared to T3 but not with T1 ($Q=20.50$, $N=8$, $p<0.001$)

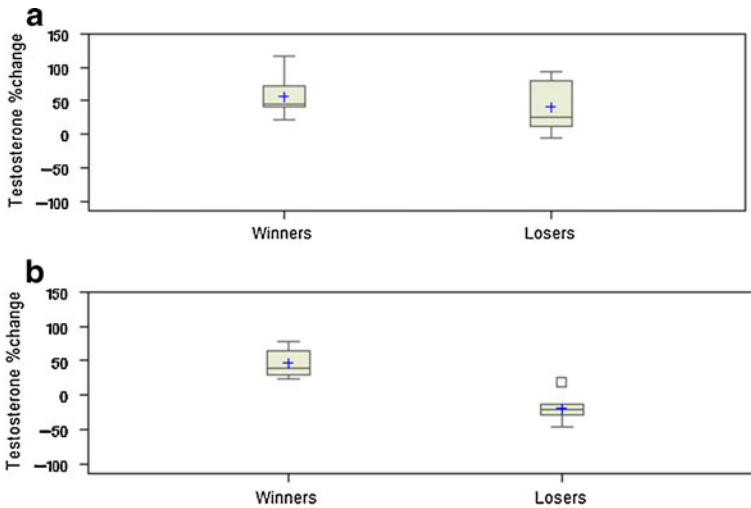


Fig. 2 **a** Percent change in testosterone immediately after the out-group competition ($Z=1.31$, $p>0.05$). No statistical differences between winners and losers percent change in T levels right after the end of the domino competition ($Z=1.31$, $p>0.05$). **b** Percent change in testosterone 30–60 min after the end of the out-group competition. Winners and losers have different trajectories of T after the out-group competition. Winners have significantly increased levels of T after 30–60 min relative to losers ($Z=3.30$, $p<0.01$). The small squares represent the maximum observation above the 75th percentile

$p>0.10$ for T3 and T4, respectively). That is, a victory against friends does not affect testosterone significantly, whereas a victory against outsiders results in elevated testosterone. Likewise, a defeat by friends has little effect on testosterone, whereas a defeat by outsiders results in decreased testosterone from pre-competition levels.

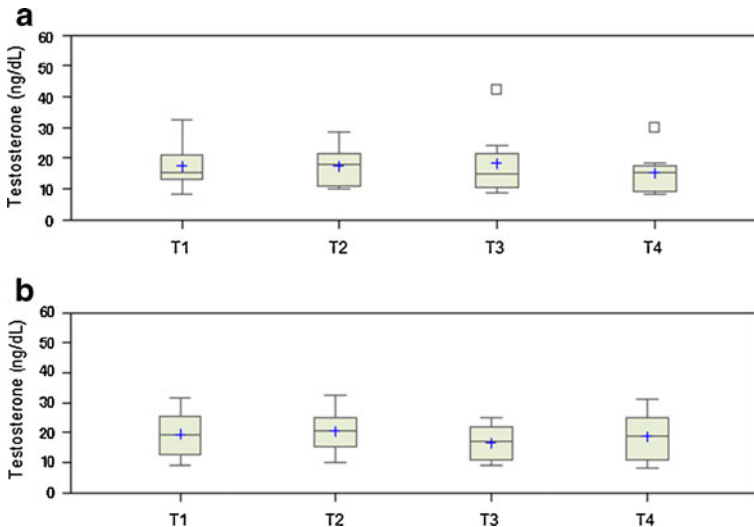


Fig. 3 **a** Testosterone levels when victorious over an in-group team. Winning against a group of friends does not have effects on T levels ($Q=4.20$, $N=8$, $p=0.24$). (T1–T4 are the same as in Fig. 1a, b.) The small squares represent the maximum observation above the 75th percentile. **b** Testosterone levels when defeated by an in-group team. Losing to a group of friends does not have effects on T levels ($Q=6.0$; $N=8$, $p=0.11$). (T1–T4 are the same as in Fig. 1a, b.)

Cricket Matches

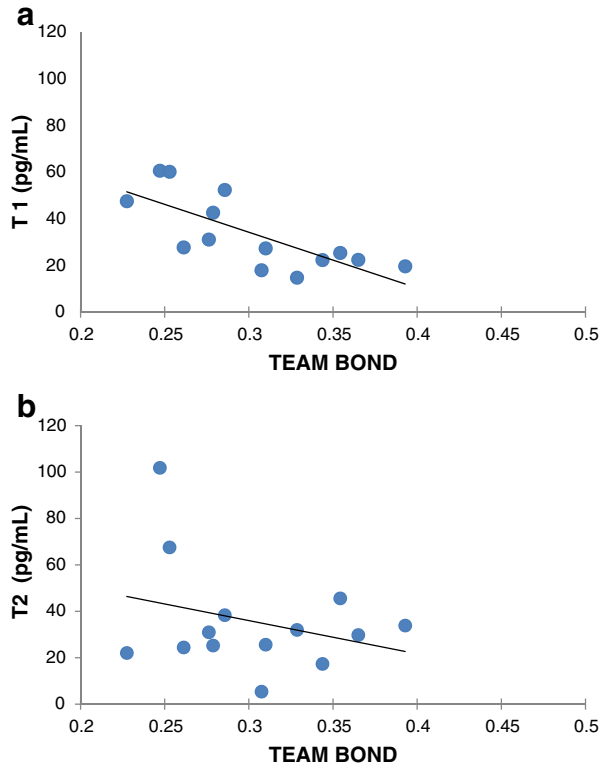
Another major venue for team competition in Bwa Mawego is the game of cricket. Children begin playing cricket at an early age with bats fashioned from palm tree fronds and using hard green fruits for balls. The rare flat plots in the otherwise rugged topography of the village are treasured as temporary cricket pitches and are often filled with neighborhood kids testing their mettle against their peers. By adolescence more structured matches occur among teams from the five major residential “hamlets” in the community that are largely kin based (for description of village geography and kinship see Quinlan and Flinn 2005). Performance in the physical and social/mental competition of cricket is often mentioned as a marker of relative status.

Percent change in salivary testosterone (post- versus pre-match) in men on a collegiate sports team has been correlated with social connectedness among teammates (i.e., those who reported higher levels of social cohesion with their teammates had larger increases in post-competition testosterone following a win) (Edwards et al. 2006). To evaluate such relationships in adolescent boys, we collected data for each player on perceived coalitionary support using a top-down successive pile sort technique (Boster 1994) during summer 2008. Nineteen teenager raters (7 from the winner team, 6 from the loser team, and 6 from the village who did not participate in the competition) were presented with 37 cards. On each card were written the first and last names of one of the 37 adolescents and young adults (ages 11 to 19 years) of the community. Each subject was asked to pile the cards based on who would support whom in case of a fight. An individual proximity matrix was built following the methods described in Anthropac for multiple sorts.² Each cell of an individual proximity matrix represents the number of times two of the 37 teenagers were placed in the same pile divided by the number of total piles the rater performed. This number represents the rater’s perceived strength of coalition support between two individuals. From each proximity matrix an aggregate matrix was built using the simple average of the 19 individual proximity matrices. Therefore each cell of the aggregate proximity matrix represents the average (from the nineteen raters) perceived strength of coalition support between two of the 37 teenagers. These procedures were performed using Ucinet 6.0 (Borgatti et al. 2002). From the aggregate proximity matrix, average strength of perceived team coalition support for each cricket player was calculated. The overall strength of team coalition support for individual i was equal to the average coalition support between i and every other teammate; we call this metric the “team bond” for individual i . Pre-match testosterone levels were highly and negatively correlated with team bond ($\rho = -0.79$, $N = 14$, $p < 0.001$; Fig. 4a) whereas post-match levels were not ($\rho = -0.02$, $N = 14$, $p > 0.10$; Fig. 4b).³

² Anthropac 4 reference manual available at <http://www.analytictech.com/anthropac/apacdesc.htm>.

³ Saliva was collected by passive drool (via use of a straw) into a 5 ml polypropylene centrifuge tube without sodium azide. Free testosterone and cortisol were quantified via an enzyme immunoassay (Salimetrics) according to manufacturer’s instructions. All individual samples were run in duplicates with standards and high and low concentration controls (controls within acceptable ranges). All samples were run in a single assay, with the intra-assay coefficient of variation equal to 3.8% and 2.3% for testosterone and cortisol respectively. One of the players of the team that lost had undetectable levels of T (below the sensitivity of the assay) before the game. This subject was not considered for further analysis concerning testosterone.

Fig. 4 a Pre-match testosterone levels and perceived coalitionary support. Pre-match T levels are associated with perceived levels of coalitionary support within own team ($\rho=-0.77$, $N=14$, $p<0.01$). **b** Post-match testosterone levels by perceived coalitionary support. Post-match T levels and perceived levels of coalitionary support within own team ($\rho=-0.02$, $N=14$, $p>0.10$)



The relation between pre-match testosterone levels and coalitionary support from teammates is particularly interesting (cf. Kivlighan et al. 2005). Our measure of coalitionary support may indicate several potential characteristics of the subject: social dominance, social competence, prosocial and cooperative behaviors toward friends, and/or being part of a larger kin network. High ratings indicate that an individual is considered an important and valuable person in his social network. This could provide a sense of security in stressful situations, such as team competitions. A trend toward a similar and statistically significant correlation was present for pre-match cortisol levels ($\rho=-0.43$, $N=15$, $p=0.10$). Alternatively, individuals who score higher in dominance might not perceive within-group challenges as important and hence have lower anticipatory testosterone levels.

Interactions with Potential Mates

Human males, similar to other mammals (e.g., Macrides et al. 1975), often elevate testosterone when interacting with potential mates (Crews and Moore 1986; Roney 2009; Roney et al. 2003, 2007; van der Meij et al. 2008). The increase in testosterone levels can be accompanied by an increase in willingness to perform physically risky tasks in the presence of female observers (Ronay and von Hippel 2010; van der Meij et al. 2011). This physiological response of increased androgens, however, may not facilitate what we have proposed is a key component of human sociality: tolerance of other males' mating relationships (Flinn et al. 2007). Therefore we would expect

testosterone levels to be high when a male is in contact with a female who is unattached, or in a relationship with someone who is not a close friend (potential mate), but we would expect the opposite—low testosterone—when interacting with a woman who is bonded with an alliance partner. Surprisingly, this hypothesis has not been investigated previously.

Analyses of testosterone levels from afternoon (12:00–18:00) saliva samples collected during focal follows and for parents of children in our stress studies from 1994 to 1999 are consistent with this supposition: when adult males are interacting with community females, they sometimes (but not always) have elevated testosterone levels, and this change is contingent upon relationship status among the male, female, and female's mating partner. That is, testosterone levels are elevated in males when interacting with potential mates but not with female relatives or females who are in relationships (wife or coresident) with close friends (Fig. 5; $Q=33.8$, $N=18$, $p<0.001$). Testosterone levels were examined by the nonparametric Friedman test in SAS. Where the Friedman statistic was significant, multiple comparison analysis with relative pairwise adjustment was used. Samples included in this analysis had been collected at the site of interaction (usually the woman's household; public locations such as rum shops were excluded) after at least 20 min from initial interaction, and not more than 20 min after the interaction ceased. Unfortunately because the samples were collected for other reasons and in a naturalistic context, we do not have sufficient appropriate samples from before the interactions to provide the basis for statistical evaluation of hormonal response (change in T levels from before to after the interaction). Anecdotally, some samples had been collected at various times during the morning prior to interaction events. In those few cases where multiple saliva samples had been collected from an individual on the same day, enabling comparison of before-and-after interaction levels, the direction of changes in T was consistent with the overall patterns.

These preliminary analyses are insufficient to evaluate alternative explanations of habituation, familiarity, or dominance/subordination (e.g., Bachman and Kummer 1980; Johnson et al. 2007; Oyegbile and Marler 2006). We do not have sufficient information on several important conditions: (1) testosterone levels before the interactions for many of the cases; (2) behaviors of females during the interactions (Storey et al. 2011); (3) feelings of threat or preparations for potential conflicts; and (4) prior frequency of interactions. Even with these important limitations, the apparent dampening of androgen levels when interacting with friends' mates is remarkable

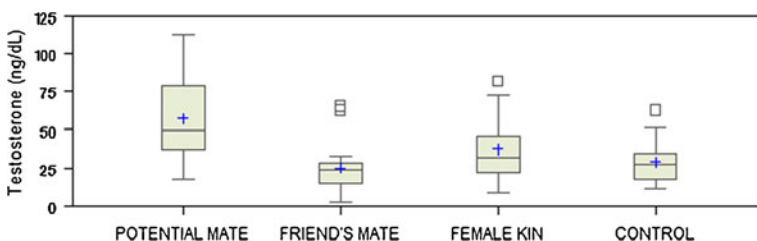


Fig. 5 Testosterone levels of adult males when interacting with females of reproductive age. Adult male testosterone levels in response to interaction with females who were resident in the community ($Q=33.8$, $N=18$, $p<0.001$). Kin category includes five sisters, three half-sisters, three close-residence first cousins

nonetheless, and consistent with mutual respect of mating relationships and enhanced cooperation among group males.

Conclusions

The human species has a paradoxical suite of coalitionary traits. We are capable of organizing into intensely cooperative groups for the purpose of horrific intergroup conflicts. Unlike our ape relatives, humans cultivate diverse and complex social relationships to form alliances among different communities. In band and tribal societies, we commonly arrange marriages between families in different kinship groupings and localities that may reciprocate for generations. Siblings usually maintain lifelong ties, even when residing in different communities. The neuroendocrine mechanisms that regulate such diverse and seemingly at-odds emotions and behaviors are complex and nuanced.

Our results suggest that testosterone levels during group competition are modulated depending on the relationships among the competitors: whether the opposition is friend or foe. Moreover males appear to respond differently to females contingent on whether they are bonded to a close friend. These results are suggestive of nuanced neuroendocrine mechanisms that are sensitive to social context, and that may be linked to the unique coalitionary behaviors of humans.

Testosterone may enable physiological and psychological responses for fighting or mating, but also for the comradeship among a “band of brothers.” Neuroendocrine mechanisms mediating conflicts of interest need to be regulated to maintain a cohesive social structure (e.g., Cikara et al. 2011). Hence testosterone reactivity may be modulated as a consequence of the respect for friends’ relationships. Of course testosterone interacts with other neuroendocrine mechanisms (oxytocinergic, serotonergic, etc.) in ways that likely modulate the long-term effects of the social interaction on neurobiology (cf. Aikey et al. 2002; Ferris 2008; Flinn et al. 2011; Heinrichs et al. 2009; Heinrichs and Domes 2008; Pedersen 2004). Perhaps this may all help to explain the apparent paradox of how extreme violence during intergroup competition is accompanied by extreme acts of altruism and social bonding within the group.

References

- Adolphs, R. (2003a). Cognitive neuroscience of human social behavior. *Nature Reviews Neuroscience*, 4, 165–178.
- Adolphs, R. (2003b). Is the human amygdala specialized for processing social information? *Annals of the New York Academy of Sciences*, 985, 326–340.
- 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, 448–460.
- Alexander, R. D. (1971). The search for an evolutionary philosophy of man. *Proceedings of the Royal Society of Victoria*, 84, 99–120.
- Alexander, R. D. (1974). The evolution of social behavior. *Annual Review of Ecology and Systematics*, 5, 325–383.
- Alexander, R. D. (1979). *Darwinism and human affairs*. Seattle: University of Washington Press.
- Alexander, R. D. (1987). *The biology of moral systems*. Hawthorne: Aldine.

- Alexander, R. D. (1990). *How did humans evolve? Reflections on the uniquely unique species*. Ann Arbor: University of Michigan Museum of Zoology Special Publication 1.
- Alexander, R. D. (1991). Social learning and kin recognition. *Ethology and Sociobiology*, 12, 387–399.
- Alexander, R. D. (2006). The challenge of human social behavior. *Evolutionary Psychology*, 4(2), 1–28.
- Alexander, R. D. (2012). Darwin's challenges and the future of human society. In F. Wayman, P. Williamson, & B. Bueno de Mesquita (Eds.), *Prediction: Breakthroughs in science, markets, and politics*. Ann Arbor: University of Michigan Press. (in press)
- Alexander, R. D., Hoogland, J. L., Howard, R. D., Noonan, K. M., & Sherman, P. W. (1979). Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates, and humans. In N. A. Chagnon & W. Irons (Eds.), *Evolutionary biology and human social behavior: an anthropological perspective* (pp. 402–435). North Scituate: Duxbury Press.
- Allman, J. M., Tetreault, N. A., Hakeem, A., & Park, S. (2011). The von Economo neurons in apes and humans. *American Journal of Human Biology*, 23, 5–21.
- Aragona, B. J., Liu, Y., Curtis, J. T., Stephan, F. K., & Wang, Z. (2003). A critical role for nucleus accumbens dopamine in partner-preference formation in male prairie voles. *Journal of Neuroscience*, 23, 3483–3490.
- Archer, J. (2006). Testosterone and human aggression: an evaluation of the challenge hypothesis. *Neuroscience and Biobehavioral Reviews*, 30, 319–345.
- Bachman, C., & Kummer, H. (1980). Male assessment of female choice in hamadryas baboons. *Behavioral Ecology and Sociobiology*, 6, 315–321.
- Bales, K. L., Kim, A. J., Lewis-Reese, A. D., & Carter, C. S. (2004). Both oxytocin and vasopressin may influence alloparental behavior in male prairie voles. *Hormones and Behavior*, 45, 354–361.
- Bartels, A., & Zeki, S. (2004). The neural correlates of maternal and romantic love. *NeuroImage*, 21, 1155–1166.
- Bateup, H. S., Booth, A., Shirtcliff, E. A., & Granger, D. A. (2002). Testosterone, cortisol, and women's competition. *Evolution and Human Behavior*, 23, 181–192.
- Beckerman, S., Erickson, P. I., Yost, J., Regalado, J., Jaramillo, L., Sparks, C., Iromenga, M., & Long, K. (2009). Life histories, blood revenge, and reproductive success among the Waorani of Ecuador. *Proceedings of the National Academy of Sciences of the USA*, 106, 8134–8139.
- Bercovitch, F. B. (2001). Reproductive ecology of old world monkeys. In P. T. Ellison (Ed.), *Reproductive ecology and human evolution* (pp. 369–396). New York: Aldine de Gruyter.
- Bernhardt, P. C., Dabbs, J. M., Fielden, J. A., & Lutter, C. D. (1998). Testosterone changes during vicarious experiences of winning among fans at sporting events. *Physiology and Behavior*, 65, 59–62.
- Bigelow, R. S. (1969). *The dawn warriors: man's evolution toward peace*. Boston: Little, Brown.
- Binmore, K. (2006). Why do people cooperate? *Politics, Philosophy & Economics*, 5, 81–96.
- Boehm, C. (1984). *Blood revenge: The anthropology of feuding in Montenegro and other tribal societies*. Lawrence: University Press of Kansas.
- Boehm, C. (1992). Segmentary 'warfare' and the management of conflict: comparison of East African chimpanzees and patrilineal-patrilocal humans. In A. H. Harcourt & F. B. M. DeWall (Eds.), *Coalitions and alliances in humans and other animals* (pp. 137–173). Oxford: Oxford Science.
- Boehm, C. (1999). *Hierarchy in the forest. The evolution of egalitarian behavior*. Cambridge: Harvard University Press.
- Boesch, C., Crockford, C., Herbinger, I., Wittig, R., Moebius, Y., & Normand, E. (2008). Intergroup conflicts among chimpanzees in Tai National Park: lethal violence and the female perspective. *American Journal of Primatology*, 70, 519–532.
- Booth, A., Shelley, G., Mazur, A., Tharp, G., & Kittok, R. (1989). Testosterone, and winning and losing in human competition. *Hormones and Behavior*, 23, 556–571.
- Borgatti, S. P., Everett, M. G., & Freeman, L. C. (2002). *Ucinet for windows: software for social network analysis*. Harvard: Analytic Technologies.
- Borries, C., Savini, T., & Koenig, A. (2011). Social monogamy and the threat of infanticide in larger mammals. *Behavioral Ecology and Sociobiology*. doi:10.1007/s00265-010-1070-5.
- Boster, J. (1994). The successive pile sort. *Field Methods*, 6(2), 11–12.
- Bowles, S. (2009). Did warfare among ancestral hunter-gatherers affect the evolution of human social behaviors? *Science*, 324, 1293–1298. doi:10.1126/science.1168112.
- Bridges, R. S. (Ed.). (2008). *Neurobiology of the parental brain*. Maryland Heights: Academic.
- Carneiro, R. (1970). A theory of the origin of the state. *Science*, 169, 733–738.
- Carter, C. S. (2002). Neuroendocrine perspectives on social attachment and love. In J. T. Cacioppo, G. G. Berntson, R. Adolphs, C. S. Carter, R. J. Davidson, M. K. McClintock, B. S. McEwen, M. J. Meaney,

- D. L. Schacter, E. M. Sternberg, S. S. Suomi, & S. E. Taylor (Eds.), *Foundations in social neuroscience* (pp. 853–890). Cambridge: MIT Press.
- Chagnon, N. A. (1968). *Yanomamö, the fierce people*. New York: Holt, Rinehart, & Winston.
- Chagnon, N. A. (1979a). Is reproductive success equal in egalitarian societies? In N. Chagnon & W. Irons (Eds.), *Evolutionary biology and human social behavior* (pp. 374–401). North Scituate: Duxbury.
- Chagnon, N. A. (1979b). Mate competition, favoring close kin, and village fissioning among the Yanomamö Indians. In N. Chagnon & W. Irons (Eds.), *Evolutionary biology and human social behavior* (pp. 86–131). North Scituate: Duxbury.
- Chagnon, N. A. (1988). Life histories, blood revenge, and warfare in a tribal population. *Science*, 239, 985–992.
- Chagnon, N. A. (2012). *The noble savage*. New York: Simon & Schuster. (in press)
- Chagnon, N. A., Flinn, M. V., & Melançon, T. (1979). Sex-ratio variation among the Yanomamö Indians. In N. Chagnon & W. Irons (Eds.), *Evolutionary biology and human social behavior* (pp. 290–320). North Scituate: Duxbury.
- Chapais, B. (2008). *Primeval kinship: How pair-bonding gave birth to human society*. Cambridge: Harvard University Press.
- Chapais, B. (2010). The deep structure of human society: Primate origins and evolution. In P. M. Kappeler & J. B. Silk (Eds.), *Mind the gap* (pp. 19–52). Berlin: Springer.
- Chapais, B. (2011). The evolutionary history of pair-bonding and parental collaboration. In C. Salmon & T. Shackelford (Eds.), *Oxford handbook of evolutionary family psychology* (pp. 33–50). New York: Oxford University Press.
- Choi, J. K., & Bowles, S. (2007). The coevolution of parochial altruism and war. *Science*, 318, 636–640.
- Cikara, M., Botvinick, M. M., & Fiske, S. T. (2011). Us versus them: Social identity shapes neural responses to intergroup competition and harm. *Psychological Science*. doi:10.1177/0956797610397667.
- Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton: Princeton University Press.
- Conner, R. C. (2010). Cooperation beyond the dyad: on simple models and a complex society. *Philosophical Transactions of the Royal Society B*, 365, 2687–2697.
- Conner, R. C., Heithaus, M. R., & Barre, L. M. (2001). Complex social structure, alliance stability and mating success in a bottlenose dolphin ‘super-alliance’. *Proceedings of the Royal Society London B*, 268, 263–267.
- Crews, D., & Moore, M. C. (1986). Evolution of mechanisms controlling mating behavior. *Science*, 231, 121–125.
- Crockett, M. J. (2009). The neurochemistry of fairness: clarifying the link between serotonin and prosocial behavior. *Annals of the New York Academy of Sciences*, 1167, 76–86.
- Crockett, M. J., Clark, L., Hauser, M. D., & Robbins, T. W. (2010). Serotonin selectively influences moral judgment and behavior through effects on harm aversion. *Proceedings of the National Academy of Sciences USA*, 107(40), 17433–17438.
- Curtis, T. J., & Wang, Z. (2003). The neurochemistry of pair bonding. *Current Directions in Psychological Science*, 12, 49–53.
- Dabbs, J. M., Jr., & Dabbs, M. G. (2000). *Heroes, rogues, and lovers: Testosterone and behavior*. New York: McGraw-Hill.
- Daly, M., & Wilson, M. (1995). Discriminative parental solicitude and the relevance of evolutionary models to the analysis of motivational systems. In M. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 1269–1286). Cambridge: MIT Press.
- de Dreu, C. K. W., Greer, L. L., Handgraaf, M. J. J., Shalvi, S., Van Kleef, G. A., Baas, M., Ten Velden, F. S., Van Dijk, E., & Feith, S. W. W. (2010). The neuropeptide oxytocin regulates parochial altruism in intergroup conflict among humans. *Science*, 328(5984), 1408–1411.
- de Dreu, C. K. W., Greer, L. L., Van Kleef, G. A., Shalvi, S., & Handgraaf, M. J. J. (2011). Oxytocin promotes human ethnocentrism. *Proceedings of the National Academy of Sciences USA*. doi:10.1073/pnas.1015316108.
- DeScioli, P., & Kurzban, R. (2009). The alliance hypothesis for human friendship. *PLoS One*, 4(6), e5802. doi:10.1371/journal.pone.0005802.
- de Waal, F. B. M. (2000). Primates: a natural heritage of conflict resolution. *Science*, 289, 586–590.
- de Waal, F. B. M. (2009). *The age of empathy: Nature’s lessons for a kinder society*. Toronto: McClelland & Stewart.
- Ditzen, B., Schaer, M., Gabriel, B., Bdenmann, G., Ehlert, U., & Heinrichs, M. (2009). Intranasal oxytocin increases positive communication and reduces cortisol levels during couple conflict. *Biological Psychiatry*, 65, 728–731.
- Domes, G., Lischke, A., Berger, C., Grossmann, A., Hauenstein, K., Heinrichs, M., & Herpertz, S. C. (2010). Effects of intranasal oxytocin on emotional face processing in women. *Psychoneuroendocrinology*, 35, 83–93.

- Edwards, D. A., & Kurlander, L. S. (2010). Women's intercollegiate volleyball and tennis: effects of warm-up, competition, and practice on saliva levels of cortisol and testosterone. *Hormones and Behavior*, 58, 606–613.
- 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, 135–143.
- Ellison, P. T., & Gray, P. (Eds.). (2009). *Endocrinology of social relationships*. Cambridge: Harvard University Press.
- Ember, C. R., & Ember, M. (1997). Violence in the ethnographic record: Records of cross-cultural research on war and aggression. In D. L. Martin & D. W. Frayer (Eds.), *Troubled times: Violence and warfare in the past* (pp. 1–20). Langhorne: Gordon & Breach.
- Fehr, E., & Fischbacher, U. (2003). The nature of human altruism. *Nature*, 425, 785–791.
- Ferris, C. (2008). Functional magnetic resonance imaging and the neurobiology of vasopressin and oxytocin. *Progress in Brain Research*, 170, 305–320.
- Fisher, H. (2002). *Why we love: The nature and chemistry of romantic love*. New York: Henry Holt and Co.
- Flinn, M. V. (2006). Evolution and ontogeny of stress response to social challenges in the human child. *Developmental Review*, 26, 138–174.
- Flinn, M. V. (2009). Are cortisol profiles a stable trait during child development? *American Journal of Human Biology*, 21(6), 769–771.
- Flinn, M. V. (2011). Evolutionary anthropology of the human family. In C. Salmon & T. Shackelford (Eds.), *Oxford handbook of evolutionary family psychology* (pp. 12–32). Oxford: Oxford University Press.
- Flinn, M. V., & Low, B. S. (1986). Resource distribution, social competition, and mating patterns in human societies. In D. Rubenstein & R. Wrangham (Eds.), *Ecological aspects of social evolution* (pp. 217–243). Princeton: Princeton University Press.
- Flinn, M. V., & Alexander, R. D. (2007). Runaway social selection. In S. W. Gangestad & J. A. Simpson (Eds.), *The evolution of mind* (pp. 249–255). New York: Guilford Press.
- Flinn, M. V., Baerwald, C., Decker, S. A., & England, B. G. (1998). Evolutionary functions of neuroendocrine response to social environment. *The Behavioral and Brain Sciences*, 21, 372–374.
- Flinn, M. V., Geary, D. C., & Ward, C. V. (2005a). Ecological dominance, social competition, and coalitionary arms races: Why humans evolved extraordinary intelligence. *Evolution and Human Behavior*, 26, 10–46.
- Flinn, M. V., Ward, C. V., & Noone, R. (2005b). Hormones and the human family. In D. Buss (Ed.), *Handbook of evolutionary psychology* (pp. 552–580). New York: Wiley.
- Flinn, M. V., Quinlan, R. J., Ward, C. V., & Coe, M. K. (2007). Evolution of the human family: Cooperative males, long social childhoods, smart mothers, and extended kin networks. In C. Salmon & T. Shackelford (Eds.), *Family relationships* (pp. 16–38). Oxford: Oxford University Press.
- Flinn, M. V., Nepomnaschy, P. A., Ponzi, D., & Muehlenbein, M. P. (2011). Evolutionary functions of early social modulation of hypothalamic-pituitary-adrenal axis development in humans. *Neuroscience and Biobehavioral Reviews*, 35(7), 1611–1629.
- Frank, S. A. (1995). Mutual policing and repression of competition in the evolution of cooperative groups. *Nature*, 377, 520–522.
- Frank, S. A. (2003). Repression of competition and the evolution of cooperation. *Evolution*, 57, 693–705.
- Frayer, D. W., & Wolpoff, M. H. (1985). Sexual dimorphism. *Annual Review of Anthropology*, 14, 429–473.
- 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, 214–219.
- Gavrilets, S., & Vose, M. D. (2006). The dynamics of Machiavellian intelligence. *Proceedings of the National Academy of Sciences USA*, 103(45), 16823–16828.
- Gavrilets, S., Duenez-Guzman, E. A., & Vose, M. D. (2008). Dynamics of alliance formation and the egalitarian revolution. *PLoS One*, 3(10), e3293.
- Geary, D. C. (2005). *The origin of mind*. Washington, DC: American Psychological Association.
- Geary, D. C. (2010). *Male, female: The evolution of human sex differences* (2nd ed.). Washington, DC: American Psychological Association.
- Geary, D. C., & Flinn, M. V. (2001). Evolution of human parental behavior and the human family. *Parenting: Science and Practice*, 1, 5–61.
- Geary, D. C., & Flinn, M. V. (2002). Sex differences in behavioral and hormonal response to social threat. *Psychological Review*, 109, 745–750.

- Gladue, B. A., Boechler, M., & McCaul, K. D. (1989). Hormonal response to competition in human males. *Aggressive Behavior*, *15*, 409–422.
- Gleason, E. D., Fuxjager, M. J., Oyegbile, T. O., & Marler, C. A. (2009). Testosterone release and social context: when it occurs and why. *Frontiers in Neuroendocrinology*, *30*(4), 460–469.
- González-Bono, E., Salvador, A., Serrano, M. A., & Ricarte, J. (1999). Testosterone, cortisol and mood in a sports team competition. *Hormones and Behavior*, *35*, 55–62.
- González-Bono, E., Salvador, A., Ricarte, J., Serrano, M. A., & Arnedo, M. (2000). Testosterone and attribution of successful competition. *Aggressive Behavior*, *26*, 235–240.
- Gould, R. V. (1999). Collective violence and group solidarity: evidence from a feuding society. *American Sociological Review*, *64*, 356–380.
- Gould, R. V. (2000). Revenge as sanction and solidarity display: an analysis of vendettas in nineteenth-century Corsica. *American Sociological Review*, *65*, 682–704.
- Gray, P. B., & Anderson, K. G. (2010). *Fatherhood: Evolution and human paternal behavior*. Cambridge: Harvard University Press.
- Hamilton, W. D. (1975). Innate social aptitudes of man: an approach from evolutionary genetics. In R. Fox (Ed.), *Biosocial anthropology* (pp. 133–153). London: Malaby Press.
- Harcourt, A. H., & de Waal, F. B. M. (1992). Co-operation in conflict: from ants to anthropoids. In A. H. Harcourt & F. B. M. de Waal (Eds.), *Coalitions and alliances in humans and other animals* (pp. 493–510). Oxford: Oxford University Press.
- Heinrichs, M., & Domes, G. (2008). Neuropeptides and social behaviour: effects of oxytocin and vasopressin in humans. *Progress in Brain Research*, *170*, 337–350.
- Heinrichs, M., von Dawans, B., & Domes, G. (2009). Oxytocin, vasopressin, and human social behavior. *Frontiers in Neuroendocrinology*, *30*, 548–557.
- Henley, C. L., Nunez, A. A., & Clemens, L. G. (2011). Hormones of choice: the neuroendocrinology of partner preference in animals. *Frontiers in Neuroendocrinology*. doi:10.1016/j.yfrne.2011.02.010.
- Henzi, S. P., Clarke, P. M. R., van Schaik, C. P., Pradhan, G. R., & Barrett, L. (2010). Infanticide and reproductive restraint in a polygynous social mammal. *Proceedings of the National Academy of Sciences USA*, *107*(5), 2130–2135.
- Hewlett, B. S. (Ed.). (1992). *Father-child relations: Cultural and biosocial contexts*. New York: Aldine de Gruyter.
- Hirschenhauser, K., & Oliveira, R. F. (2006). Social modulation of androgens in male vertebrates: meta-analyses of the challenge hypothesis. *Animal Behavior*, *71*, 265–277.
- Hughes, A. L. (1988). *Evolution and human kinship*. Oxford: Oxford University Press.
- Hrdy, S. B. (1999). *Mother Nature: A history of mothers, infants, and natural selection*. New York: Pantheon.
- Hrdy, S. B. (2009). *Mothers and others: The evolutionary origins of mutual understanding*. Cambridge: Harvard University Press.
- Jacoby, S. (1983). *Wild justice: The evolution of revenge*. New York: Harper & Row.
- Johnson, R. T., Burk, J. A., & Kirkpatrick, L. A. (2007). Dominance and prestige as differential predictors of aggression and testosterone levels in men. *Evolution and Human Behavior*, *28*, 345–351.
- Keeley, L. (1996). *War before civilization*. New York: Oxford University Press.
- Kivlighan, K. T., Granger, D. A., & Booth, A. (2005). Gender differences in testosterone and cortisol response to competition. *Psychoneuroendocrinology*, *30*, 58–71.
- Knauff, B. B. (1991). Violence and sociality in human evolution. *Current Anthropology*, *32*, 391–428.
- Kosfeld, M., Heinrichs, M., Zak, P. J., Fischbacher, U., & Fehr, E. (2005). Oxytocin increases trust in humans. *Nature*, *435*, 673–676.
- Kurzban, R., & Neuberg, S. (2005). Managing ingroup and outgroup relationships. In D. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 653–675). Hoboken: Wiley.
- Lamb, M. E. (2004). *The role of the father in child development*. New York: Wiley.
- LeBlanc, S. A. (2003). *Constant battles: The myth of the peaceful, noble savage*. New York: St. Martin's Press.
- Lee, H.-J., Macbeth, A. H., Pagani, J. H., & Young, W. S., III. (2009). Oxytocin: the great facilitator of life. *Progress in Neurobiology*, *88*, 127–151.
- Macrides, F., Bartke, A., & Dalterio, S. (1975). Strange females increase plasma testosterone levels in male mice. *Science*, *189*, 1104–1106.
- Maner, J. K., Miller, S. L., Schmidt, N. B., & Eckel, L. A. (2008). Submitting to defeat: social anxiety, dominance threat, and decrements in testosterone. *Psychological Science*, *19*, 764–768.
- Manson, J. H., & Wrangham, R. (1991). Intergroup aggression in chimpanzees and humans. *Current Anthropology*, *32*(4), 369–390.

- Marlowe, F. W. (2010). *The Hadza: Hunter-gatherers of Tanzania*. Berkeley: University of California Press.
- Mazur, A., Booth, A., & Dabbs, J. M. (1992). Testosterone and chess competition. *Social Psychology Quarterly*, 55, 70–77.
- McHenry, H. M. (1992). Body size and proportions in early hominids. *American Journal of Physical Anthropology*, 87, 407–431.
- Mehta, P. H., Wuchrman, E. A., & Josephs, R. A. (2009). When are low testosterone levels advantageous? The moderating role of individual versus intergroup competition. *Hormones and Behavior*, 56, 158–162.
- Miller, G. (2010). The prickly side of oxytocin. *Science*, 328, 1343.
- Mitani, J. C., Watts, D. P., & Amstler, S. J. (2010). Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Current Biology*, 20, R507–R508.
- Muehlenbein, M. P. (2008). Adaptive variation in testosterone levels in response to immune activation: empirical and theoretical perspectives. *Social Biology*, 53, 13–23.
- Muehlenbein, M. P., & Flinn, M. V. (2011). Patterns and processes of human life history evolution. In T. Flatt & A. Heyland (Eds.), *Oxford handbook of life history* (pp. 153–168). Oxford: Oxford University Press.
- Muehlenbein, M. P., Hirschtick, J. L., Bonner, J. Z., & Swartz, A. M. (2010). Towards quantifying the usage costs of human immunity: altered metabolic rates and hormone levels during acute immune activation in men. *American Journal of Human Biology*, 22, 546–556.
- Muller, M. N., Thompson, M. E., Kahlenberg, S. M., & Wrangham, R. W. (2011). Sexual coercion by male chimpanzees shows that female choice may be more apparent than real. *Behavioral Ecology and Sociobiology*. doi:10.1007/s00265-010-1093-y.
- Nesse, R. M. (2007). Runaway social selection for displays of partner value and altruism. *Biological Theory*, 2, 143–155.
- Nowak, M. (2006). Five rules for the evolution of cooperation. *Science*, 314, 1560–1563.
- Oliveira, T., Gouveia, M. J., & Oliveira, R. F. (2009). Testosterone responsiveness to winning and losing experiences in female soccer players. *Psychoneuroendocrinology*, 34, 1056–1064.
- Ophir, A. G. (2011). Towards meeting Tinbergen's challenge. *Hormones and Behavior*. doi:10.1016/j.yhbeh.2011.03.012.
- Ostner, J., Heistermann, M., & Schülke, O. (2011). Male competition and its hormonal correlates in Assamese macaques (*Macaca assamensis*). *Hormones and Behavior*, 59(1), 105–113.
- Otterbein, K. F. (1994). *Feuding and warfare: Selected works of Keith F. Otterbein*. Langhorne: Gordon and Breach.
- Oxford, J., Ponzi, D., & Geary, D. C. (2010). Hormonal responses differ when playing violent video games against an in-group and outgroup. *Evolution and Human Behavior*, 31, 201–209.
- Oyegbale, T. O., & Marler, C. A. (2006). Weak winner effect in a less aggressive mammal: correlations with corticosterone but not testosterone. *Physiology and Behavior*, 89, 171–179.
- Palombit, R. A. (1994). Dynamic pair bonds in Hylobatids: implications regarding monogamous social systems. *Behaviour*, 128(1–2), 65–101.
- Panksepp, J. (2009). Primary process affects and brain oxytocin. *Biological Psychiatry*, 65, 725–727.
- Pedersen, C. A. (2004). Biological aspects of social bonding and the roots of human violence. *Annals of the New York Academy of Sciences*, 1036, 106–127.
- Plavcan, J. M. (2012). Sexual size dimorphism, canine dimorphism, and male-male competition in primates: where do humans fit in? *Human Nature*, 23. doi:10.1007/s12110-012-9130-3.
- Plavcan, J. M., & van Schaik, C. P. (1997). Intrasexual competition and body size dimorphism in anthropoid primates. *American Journal of Physical Anthropology*, 103, 37–68.
- Plavcan, J. M., van Schaik, C. P., & Kappeler, P. M. (1995). Competition, coalitions and canine size in primates. *Journal of Human Evolution*, 3, 245–276.
- Plavcan, J. M., Lockwood, C. A., Kimbel, W. H., Lague, M. R., & Harmon, E. H. (2005). Sexual dimorphism in *Australopithecus afarensis* revisited: How strong is the case for a human-like pattern of dimorphism? *Journal of Human Evolution*, 48, 313–320.
- Quinlan, R. J. (2008). Human pair-bonds: evolutionary functions, ecological variation, and adaptive development. *Evolutionary Anthropology*, 17, 227–238.
- Quinlan, R. J., & Flinn, M. V. (2005). Kinship, sex & fitness in a Caribbean community. *Human Nature*, 16(1), 32–57.
- Reno, P. L., Meindl, R. S., McCollum, M. A., & Lovejoy, C. O. (2003). Sexual dimorphism in *Australopithecus afarensis* was similar to that of modern humans. *Proceedings of the National Academy of Sciences USA*, 100, 9404–9409.
- Ridley, M. (1996). *The origins of virtue*. New York: Viking (Penguin Books).
- Rilling, J. K., & Sanfey, A. G. (2011). The neuroscience of social decision-making. *Annual Review of Psychology*, 62, 23–48.

- Rodseth, L., & Wrangham, R. W. (2004). Human kinship: A continuation of politics by other means? In B. Chapais & C. Berman (Eds.), *Kinship and behavior in primates* (pp. 389–419). New York: Oxford University Press.
- Rodseth, L., Wrangham, R., Harrigan, A., & Smuts, B. (1991). The human community as primate society. *Current Anthropology*, 32, 221–254.
- Roney, J. R. (2009). The role of sex hormones in the initiation of human mating relationships. In P. T. Ellison & P. B. Gray (Eds.), *The endocrinology of social relationships* (pp. 246–269). Cambridge: Harvard University Press.
- Ronay, R., & von Hippel, W. (2010). The presence of an attractive woman elevates testosterone and physical risk taking in young men. *Social Psychological and Personality Science*, 1, 57–64.
- Roney, J. R., Mahler, S. V., & Maestripieri, D. (2003). Behavioral and hormonal responses of men to brief interactions with women. *Evolution and Human Behavior*, 24, 365–375.
- Roney, J. R., Lukaszewski, A. W., & Simmons, Z. L. (2007). Rapid endocrine responses of young men to social interactions with young women. *Hormones and Behavior*, 52, 326–333.
- Salvador, A. (2005). Coping with competitive situations in humans. *Neuroscience and Biobehavioral Reviews*, 29, 195–205.
- Salvador, A., & Costa, R. (2009). Coping with competition: neuroendocrine responses and cognitive variables. *Neuroscience and Biobehavioral Reviews*, 33, 160–170.
- Salvador, A., Simon, V., Suay, F., & Llorens, L. (1987). Testosterone and cortisol responses to competitive fighting in human males. *Aggressive Behavior*, 13, 9–13.
- 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, 365–375.
- Schultheiss, O., Campbell, K., & McClelland, D. (1999). Implicit power motivation moderates men's testosterone responses to imagined and real dominance success. *Hormones and Behavior*, 36, 234–241.
- Shaller, M., & Neuberg, S. (2008). Intergroup prejudices and intergroup conflicts. In C. Crawford & D. L. Krebs (Eds.), *Foundations of evolutionary psychology* (pp. 401–414). Mahwah: Erlbaum.
- Shamay-Tooory, S. G., Fischer, M., Dvash, J., Harari, H., Perach-Bloom, N., & Levkovitz, Y. (2009). Intranasal administration of oxytocin increases envy and schadenfreude (gloating). *Biological Psychiatry*, 66, 864–870.
- Siegel, S., & Castellan, N. J. (1988). *Nonparametric statistics for the behavioral sciences*. McGraw-Hill Publishing Co.
- Soliani, L. (2008). *I test non parametrici piu' citati nelle discipline scientifiche*. Universita' degli studi di Parma.
- Stevens, J. R., Cushman, F. A., & Hauser, M. D. (2005). Evolving the psychological mechanisms for cooperation. *Annual Review of Ecology and Systematics*, 36, 499–518.
- Storey, A. E., Walsh, C. J., Quinton, R. L., & Wynne-Edwards, K. E. (2000). Hormonal correlates of paternal responsiveness in new and expectant fathers. *Evolution and Human Behavior*, 21, 79–95.
- Storey, A.E., Noseworthy, D.E., Delahunty, K.M., Halfyard, S.J., McKay, D.W. (2011). The effects of social context on the hormonal and behavioral responsiveness of human fathers. *Hormones and Behavior*, 60, 353–361.
- Theodoridou, A., Rowe, A. C., Penton-Voak, I. S., & Rogers, P. J. (2009). Oxytocin and social perception: oxytocin increases perceived facial trustworthiness and attractiveness. *Hormones and Behavior*, 56, 128–132.
- Tiger, L. (1969). *Men in groups*. New York: Random House.
- Tiger, L., & Fox, R. (1971). *The imperial animal*. New York: Holt, Rinehart and Winston.
- Tinbergen, N. (1963). On aims and methods in ethology. *Zeitschrift für Tierpsychologie*, 20, 410–433.
- Trivers, R. L. (1971). The evolution of reciprocal altruism. *The Quarterly Review of Biology*, 46, 35–57.
- Trumble, B. C., Cummings, D. K., von Rueden, C. R., O'Connor, K. A., Gurven, M. D., & Kaplan, H. S. (2011). Changes in male salivary testosterone in response to competitive soccer matches among the Tsimane of the Bolivian Amazon. *American Journal of Human Biology*, 23, 281.
- Tse, W. S., & Bond, A. J. (2002). Serotonergic intervention affects both social dominance and affiliative behaviour. *Psychopharmacology*, 161, 324–330.
- Ulrich-Lai, Y. M., & Herman, J. P. (2009). Neural regulation of endocrine and autonomic stress responses. *Nature Reviews Neuroscience*, 10, 397–409.
- van der Meij, L., Buunk, A. P., van de Sande, J. P., & Salvador, A. (2008). The presence of a woman increases testosterone in aggressive dominant men. *Hormones and Behavior*, 54, 640–644.
- van der Meij, L., Almela, M., Buunk, A. P., Fawcett, T. W., & Salvador, A. (2011). Men with elevated testosterone levels show more affiliative behaviours during interactions with women. *Proceedings of the Royal Society London B*. doi:10.1098/rspb.2011.0764.
- van Vugt, M., de Cremer, D., & Janssen, D. P. (2007). Gender differences in cooperation and competition. *Psychological Science*, 18, 19–23.

- Veldhuis, J. D., & Iranmanesh, A. (2004). Pulsatile intravenous infusion of recombinant human luteinizing hormone under acute gonadotropin-releasing hormone receptor blockade reconstitutes testosterone secretion in young men. *Journal of Clinical Endocrinology and Metabolism*, *89*, 4474–4479.
- Wagner, J. D., Flinn, M. V., & England, B. G. (2002). Hormonal response to competition among male coalitions. *Evolution and Human Behavior*, *23*(6), 437–442.
- Walker, P. L. (2001). A bioarchaeological perspective on the history of violence. *Annual Review of Anthropology*, *30*, 573–596.
- Walker, R. S., Flinn, M. V., & Hill, K. R. (2010). Evolutionary history of partible paternity in lowland South America. *Proceedings of the National Academy of Sciences USA*, *107*, 19195–19200.
- Walker, R. S., Hill, K. R., Flinn, M. V., & Ellsworth, R. M. (2011). Evolutionary history of hunter-gatherer marriage practices. *PLoS One*, *6*(4), e19066. doi:10.1371/journal.pone.0019066.
- Warneken, F., & Tomasello, M. (2009). Varieties of altruism in children and chimpanzees. *Trends in Cognitive Sciences*, *13*, 397–402.
- Watts, D. P. (1996). Comparative socio-ecology of gorillas. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 16–28). Cambridge: Cambridge University Press.
- Watts, D. P. (1998). Coalitionary mate-guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology*, *44*, 43–55.
- Watts, D. P., Muller, M., Amsler, S. J., Mbabazi, G., & Mitani, J. C. (2006). Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda. *American Journal of Primatology*, *68*, 161–180.
- Wiessner, P. (2002). Hunting, healing, and Hxaro exchange: a long-term perspective on !Kung (Ju/'hoansi) large-game hunting. *Evolution and Human Behavior*, *23*, 407–436.
- Wingfield, J. C., Hegner, R. E., Duffy, A. M., Jr., & Ball, G. F. (1990). The “challenge hypothesis”: theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *American Naturalist*, *136*, 829–846.
- Wobber, V., Hare, B., Maboto, J., Lipson, S., Wrangham, R., & Ellison, P. T. (2010). Differential changes in steroid hormones before competition in bonobos and chimpanzees. *Proceedings of the National Academy of Sciences USA*, *107*, 12457–12462.
- Wrangham, R. W. (1999). Evolution of coalitional killing. *Yearbook of Physical Anthropology*, *42*, 1–30.
- Wrangham, R. W., & Peterson, D. (1996). *Demonic males*. New York: Houghton Mifflin Company.
- Wrangham, R. W., & Glowacki, L. (2012). Intergroup aggression in chimpanzees and war in nomadic hunter-gatherers: evaluating the chimpanzee model. *Human Nature*, *23*. doi:10.1007/s12110-012-9132-1.
- Wright, R. (1994). *The moral animal*. New York: Random House (Pantheon).
- Wu, X.-J., Schepartz, L. A., Liu, W., & Trinkaus, E. (2011). Antemortem trauma and survival in the late Middle Pleistocene human cranium from Maba, South China. *Proceedings of the National Academy of Sciences USA*. doi:10.1073/pnas.1117113108.
- Young, K. A., Gobrogge, K. L., Liu, Y., & Wang, Z. (2011). The neurobiology of pair bonding: Insights from a socially monogamous rodent. *Frontiers in Neuroendocrinology*, *32*, 53–69.
- Young, L. J., & Insel, T. R. (2002). Hormones and parental behavior. In J. B. Becker, S. M. Breedlove, D. Crews, & M. M. McCarthy (Eds.), *Behavioral endocrinology* (pp. 331–369). Cambridge: MIT Press.
- Zak, P. J., Kurzban, R., & Matzner, W. T. (2005). Oxytocin is associated with human trustworthiness. *Hormones and Behavior*, *48*, 522–527.
- Zak, P. J., Kurzban, R., Ahmadi, S., Swerdloff, R. S., Park, J., Efrimidze, L., Redwine, K., Morgan, K., & Matzner, W. T. (2009). Testosterone administration decreases generosity in the ultimatum game. *PlosOne*, *4*(12), 1–7.

Mark V. Flinn is a professor in the Department of Anthropology at the University of Missouri. For the past twenty-three years he has studied child stress and health in a rural community on the island of Dominica. His research involves monitoring hormone levels to examine what factors affect neuroendocrine responses in children's everyday lives. He is the president-elect of the Human Behavior and Evolution Society.

Davide Ponzi recently received his PhD in neurobiology with an interdisciplinary project embracing biological anthropology and developmental psychology at the University of Missouri. His research targets the long-term effects of early exposure to environmental adversities on the psychobiological development of an organism using animal models of endocrine disruption and development of the stress system in children. He is interested in early-life individual differences in stress sensitivity and resilience, the development of behavioral and cognitive sex differences, and ingroup-outgroup behaviors. His research integrates methodologies from anthropology, behavioral neuroendocrinology, and behavioral neuroscience.

Michael Muehlenbein is an assistant professor of anthropology at Indiana University, Bloomington. His research is focused on various aspects of evolutionary endocrinology and ecological immunology in humans, monkeys, and apes. He is particularly interested in describing relationships among hormones and immune measures; phenotypic signals, such as coloration/symmetry/digit ratio; cooperative/parental/competitive/risk-taking/health behaviors; and social/physical development. Other interests include immune and endocrine assay development and infectious disease diagnostics.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.