ENDOCRINE CRONIES: MALE COALITIONS AND HORMONE RESPONSE TO COMPETITION

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ABSTRACT

This study investigates hormone response to competition and male coalitions. Coalitionary aggression may represent a fundamental human adaptation (Alexander, 1989; Wrangham, 1999). Males have complex hormone responses to competitive events (Elias 1981; Dabbs & Dabbs, 2000) that may have important effects on psychological and behavioral mechanisms involved in coalitionary competition. Within- and between-group competitions probably engage different types of mechanisms.

Salivary testosterone (T) and cortisol (C) levels were assessed in adult males from a rural Caribbean village who competed at domino against (a) familiar men from their own village (within coalition) and (b) strangers from another village (between coalitions). Analyses of data indicate that salivary T and especially C levels were more elevated for between-coalition competition than for within-coalition competition. These findings suggest that male coalitions are an important contextual factor modulating hormone response to competition.

Chapter One: Introduction

> Why are we all alone at the pinnacle of the particular direction of rapid evolutionary change that led to the combining of such traits as a huge brain, complex intellect, upright posture, concealed ovulation, menopause, virtual hairlessness, a physically helpless but mentally precocial baby and *above all our tendency and ability to cooperate and compete in social and political groups of millions?* (Italics mine).

- Alexander, 1990

> **co·ali·tion** \ko′-e-lish-en\ *n* **1 a :** the act of coalescing :UNION **b :** a body formed by the coalescing of orig. distinct elements : COMBINATION **2 :** a temporary alliance of distinct parties, persons, or states for joint action

- Webster's New Collegiate Dictionary, 1973

This study investigates male coalitions and hormone response to competition in rural Caribbean males. The primary objective is to determine if hormone response is different depending on whether competition occurs within one's coalition or against an outside coalition. This difference is considered to be theoretically important given the role of coalitionary competition in human evolution (Alexander, 1979–90).

Humans respond to physical (wrestling, judo, basketball) and mental (chess, computer games) challenges with complex hormone responses. Testosterone (T) is the primary androgen and has wide-ranging effects on mood, libido, immunity, and energy allocation (Booth, Johnson, & Granger, 1999b; Dabbs & Dabbs, 2000; Campbell, Lukas, & Campbell, 2001; Mooradian, Morley, & Korenman, 1987; Rubinow & Schmidt, 1996). T tends to increase in those experiencing success or victory relative to those experiencing defeat (Elias, 1981; Mazur & Lamb, 1980). T also mediates dominance-related behaviors in primates (Mazur, 1985) and humans (Mazur & Booth, 1998), increasing in those experiencing a rise in status and falling in those showing deference.

Most studies of human hormone response to competition have focused on dyadic interactions. However, humans frequently compete as groups and engage in extensive coalitionary competition (Alexander, 1979–90). By merging Humphrey's (1976) model of the brain as a social tool with balance-of-power models of hominid social organization (e.g., Manson & Wrangham, 1991), Alexander posited a codified model of recent human evolution that potentially accounts for many unique characteristics of our species including increased parental care, altricial infants, large social groups, increased social cognition, and menopause, among others. The "engine" in this model is the advent of sustained intergroup competition, or social competition (Geary & Flinn, 2001; Ward & Flinn, 2001), among sub-populations of hominids that set up arms races among coalitions and selected for group solidarity and increased social complexity. As a result, individuals became embedded in nested coalitions, structured around kin groups, where individual success depended on group success. With this change, group dynamics also changed; Male reproductive success, for example, became increasingly dependent on securing allies and the cooperation of other males rather than simply dominating them. The emergence of extensive coalitionary competition generated two qualitatively different arenas of social competition—within and between groups—which likely required different competitive and/or cooperative mechanisms (Geary & Flinn, in press).

Cooperation and competition may involve hormone mechanisms that affect cognition and behavior. T response to competition is a meaningful index of dominance behavior and C level is indicative of an organism's state of arousal. The permissive effects of C on other hormones (Sapolsky, Romero, & Munck, 2000) suggest that the interactions of T and C may also be important. T/C ratio has been positively correlated with athletic performance in swimmers (Mujika et al., 1996) and also affects psychological response to stress (Moya-Albiol et al., 2001). Both T and C influence thought patterns and behavior in profound and complex ways (Dabbs & Dabbs, 2000; McEwen & Sapolsky, 1995).

To investigate the influence of coalitionary context on hormone response to competition, fieldwork was conducted over a two-week period in a small village on the island of Dominica. First, information on men's social status and coalitionary networks was gathered. Then, a small group of men was selected to participate in domino matches among themselves and then against men from another village. Hormone levels were assessed from saliva collected before and after matches. Results indicate that levels of both hormones—and particularly cortisol—were much more elevated during between-coalition competition in this sample. These findings suggest that the context of male coalitions significantly modifies hormone response to competition in this population.

Overview of Thesis

This thesis is divided into six chapters. Chapter one sketches the research problem and places it within the larger theoretical context. Chapter two provides basic hormone principles, reviews the functions of T and C, presents relevant research, and discusses the role of coalitionary behavior for human evolution. Chapter three provides background information on Dominica and the village of Bwa Mawego. Chapter four presents methods for information collection, study design, and data analyses. Results are presented in chapter five—brief narrative accounts of domino matches are followed by hormone profiles and tests of the hypotheses. Chapter six discusses the findings, strengths and limits of the study, and directions for future research.

Chapter Two: Testosterone, Cortisol, and Coalitions

Hormone Classification and Actions

A hormone is a substance produced by a gland that is carried by the circulatory system to a target organ, where it causes an effect (Becker & Breedlove, 1992: 23). Hormones are traditionally categorized according to their chemical structure, with the major division being between protein, or peptide-based, hormones and steroid hormones. Protein-based hormones include the amines, which are single amino acids, and the polypeptides, which are made up of a number of amino acids. Steroid hormones are derived from cholesterol and are divided into six categories: estrogens (female sex steroids), androgens (male sex steroids), progestins, mineralocorticoids, glucocorticoids, and vitamin D and its daughter metabolites (Becker & Breedlove, 1992: 31; Norman & Litwack, 1997: 51). The discovery of new hormones (approximately 130 to date) has expanded these categories. For example, prostaglandins are hormones derived from fatty acids and do not, as such, fall into any of the categories mentioned above (Norman & Litwack, 1997: 3).

No clear dividing line exists between a hormone and a neurotransmitter. For example, epinephrine traditionally is classified as a hormone and norepinephrine as a neurotransmitter. But the similarity in structure and activities has led some investigators to classify these substances according to their range of influence. Substances acting over long distances are classified as endocrine hormones, and substances acting over shorter distances are classified as paracrine hormones. Opoids and enkephalins are possible paracrine hormones. Autocrines are another class of hormones that act on the same cell from which they are produced and may also affect adjacent cells. Prostaglandins are examples of autocrine hormones. However, even this division between hormones is not entirely accurate because hormones can have effects over multiple ranges (Norman & Litwack, 1987: 2–3). It is increasingly accepted that neurotransmitters are really hormones that act quickly over short distances, and therefore they would be classified as paracrine hormones (Norman & Litwack, 1997: 6–7). In sum, organisms use a large number of chemical messengers acting over various ranges and at different speeds to communicate among cells.

One organ affected by hormone action is the brain, and it is here that hormone function is regulated. Of particular importance is the hypothalamus, a small area located at the base of the forebrain just above the roof of the mouth. The hypothalamus serves as the neural control center for all vertebrate endocrine systems and, as such, exerts a profound influence on the secretion of nearly every known hormone. Within the hypothalamus there are a number of specialized nuclei, or functional groups of neurons, that are involved in the regulation and integration of endocrine and physiological functions and behaviors (Becker & Breedlove, 1992: 23–24). These neurons release their products directly into the circulatory system rather than into a neuronal synapse, as do most neurons.

The pituitary gland is located just beneath the hypothalamus and is attached to it by a slender stalk. Perhaps the most important of all endocrine glands, the pituitary has a posterior and an anterior lobe, each of which receives information from the hypothalamus differently. The anterior lobe (or adenohypophysis) receives signals from the hypothalamus via the hypophyseal portal blood vessels (HPV), a thin network of arteries that supplies the pituitary with blood and chemical messengers from hypothalamic nuclei and the general circulatory system. In response to an environmental signal or internal stimulus, substances are released from the hypothalamic nuclei and cause the pituitary to secrete hormones. These substances, called releasing factors, are peptide hormones that trigger specific nuclei in the pituitary to release preformed hormone into the blood. Hormones released from the pituitary are also peptide hormones and act as secondary messengers. They are carried by the circulatory system to endocrine organs, where they attach to cell membranes and signal that organ to begin secreting the ultimate, or target, hormone. Essentially this process operates as an enormous cascade system by which a very small amount of substance (the releasing factor hormone from the hypothalamic nuclei) is converted into large amounts of active hormone (Norman & Litwack, 1997: 9).

The other lobe of the pituitary gland, the posterior, does not receive signals through the HPV blood system, as does the anterior pituitary lobe, but is directly innervated by the hypothalamus. Signals from the hypothalamic nuclei are transmitted along axons projecting directly into the posterior pituitary. When stimulated, posterior-pituitary nuclei release hormones directly into the general circulation, with no intervening messengers, and also release hormones directly into the brain and spinal cord, where they act as neurotransmitters. Examples of hormones released in this fashion are oxytocin and vasopressin.

The body uses feedback loops to monitor hormone levels, and it is here that intermediate messenger hormones are important. A positive-feedback loop describes a situation in which one hormone causes another hormone to increase its secretion, which in turn causes the original hormone to increase its secretion further, and so on. Negative-feedback loops are much more common in biological systems, and here an increase in one hormone triggers a set of reactions that restricts the further release of that hormone. The central nervous system (CNS), hypothalamus, anterior pituitary, and target organs are all involved in various inhibitory feedback loops that act at different speeds.

In general, the anterior pituitary feeds back negatively on the hypothalamus in a short feedback loop. Longer feedback loops occur between ultimate hormones and structures higher up in the cascade. These hormones operate directly on the anterior pituitary, the hypothalamus, and the CNS.

Hormones travel in the blood either in free form or bound to carrier molecules. Most peptide hormones circulate in free form, except for glycoproteins, which are bound to a sugar group (the “glyco” prefix is from glycogen, the basic building block of sugar, Becker & Breedlove, 1992: 30). Because protein hormones are not lipid-soluble, they must be packaged in vesicles for transport into and out of cells. On reaching a target cell, specific receptor molecules in the outer-cell membrane either import the hormone or become activated and trigger a series of intracellular chemical reactions.

Steroid hormones, however, are lipid-soluble and can freely cross lipid cell membranes, including the blood-brain barrier. Therefore, their level in the bloodstream is governed only by their rate of synthesis (Becker & Breedlove, 1992: 30). Nonetheless, steroids often are bound to carrier proteins, which prevent them from crossing cell membranes. Carrier proteins for steroids come in two varieties: nonspecific, such as albumin, and highly specific, such as sex-hormone-binding globulin (SHBG) or corticosteroid-binding globulin (CBG) (Ellison, 1988). Specific globulin binds steroids more strongly than albumin.

Only free, or unbound, steroid is considered biologically active and only around 1-3% exists in this form (Griffin, 2000a: 120). However, albumin-bound hormones are readily available for transport into cells where they rapidly dissociate from their protein carriers in capillary beds (Griffin, 2000a: 120). To achieve accurate measures of biologically active hormones a measure of binding proteins may be necessary, or ideally, a method for measuring hormone-carrier dissociation rates. After diffusing into a cell, steroid hormones bind to specific steroid-receptor proteins, and this complex in turn binds to DNA. Thus, steroids are able to regulate gene transcription, or expression.

Testosterone

Testosterone (T) is the primary androgen, or male sex hormone, and is produced primarily by the Leydig cells, located in testes, although small amounts are produced in both sexes by the adrenal glands, located just above the kidneys. Known functions of androgens include sexual differentiation of the male phenotype *in utero*; promotion of male secondary sex characteristics during puberty; stimulation of spermatogenesis; regulation of gonadotropin (intermediate peptide) hormone secretion by the hypothalamic-pituitary system; and actions on the central nervous system (CNS) and brain (Griffin 2000b: 249; Norman & Litwack, 1997: 347). T secretion is regulated via the hypothalamic-pituitary-testicular axis (HPT) (Figure 2.1).

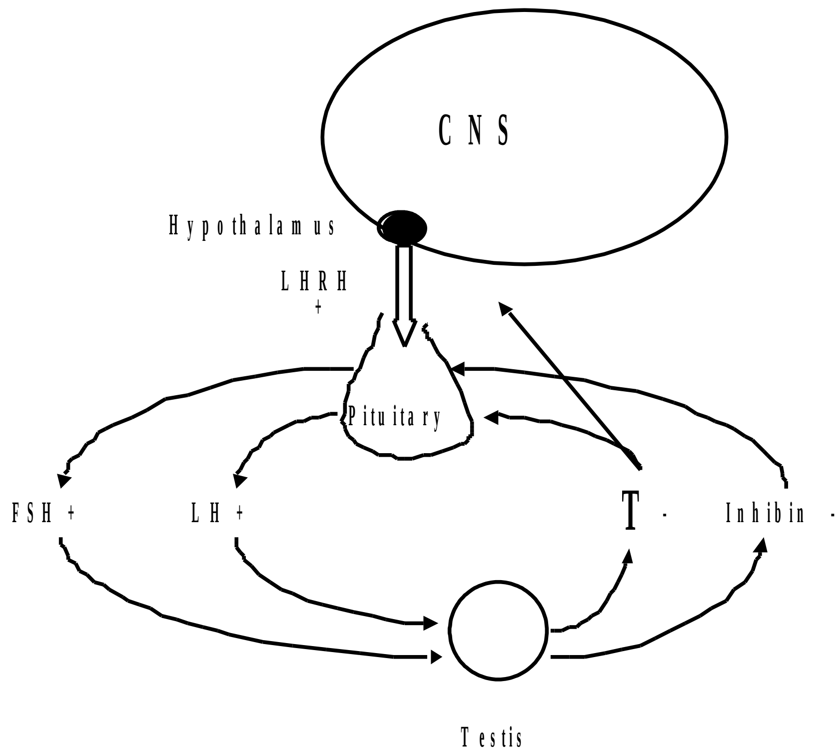

Figure 2.1 Hypothalamic-pituitary-testicular axis.

The hypothalamus secretes luteinizing-hormone-releasing hormone (LHRH, also called gonadotropin-releasing hormone [GnRH]), which in turn stimulates the pituitary to secrete luteinizing hormone (LH) and follicle-stimulating horomone (FSH). LH travels by way of the circulatory system to the testes, where it stimulates Leydig cells to secrete T. Normal sperm production requires FSH and T. Plasma T then inhibits further release of LHRH from the hypothalamus and LH from the pituitary. T inhibits further production of FSH by way of the hypothalamus, although inhibin appears to be the gonadal hormone of greatest importance for feedback control at the level of the pituitary (Griffin, 2000b). T circulates in plasma largely bound to albumin and SHBG (sometimes called testosterone-binding globulin [TeBG]). About 2% of T is unbound, with 44% bound to SHBG and 54% bound to albumin (Griffin, 2000b: 247). When T enters a cell it binds the receptor in free form or after conversion to dihydrotestosterone (DHT) by 5-alpha-reductase. DHT is a much more potent agent than is T–DHT binds receptor more tightly and the DHT-receptor-complex also binds chromatin more efficiently. Cells vary in how much androgen receptor they contain and, hence, in how much they are affected by the actions of T.

T exerts profound effects on the developing fetus. Sexual organs become differentiated between the seventh and fifteenth weeks of pregnancy in response to increased T (and a peptide hormone known as müllerian regression factor) production by the fetus. T and its metabolites also affect cognitive development *in utero* by influencing rates of cerebral growth and lateralization. Specifically, T has been linked to increased prenatal growth in the right hemisphere and decreased lateralization (Geschwind & Galaburda, 1987; Kimura, 1987; 1999).

For boys, T is low at birth but increases during the first six months before dropping once again by one year of age (Norman & Litwack, 1997). Around age 7, adrenal androgen production increases and stimulates a prepubertal growth spurt, although overall levels of plasma (or blood) T remain low (Griffin, 2000b: 256). The onset of puberty (about 10 years of age for human males) is marked by steadily increasing plasma T levels, which initiate the development of male secondary sexual characteristics such as skeletal and muscle growth, deepening of voice, hair growth and distribution, and development of libido (Norman & Litwack, 1997: 347). T levels peak around 17 years of age and then steadily decline (Dabbs, 1990a).

During growth and development, T exerts organizational effects that permanently alter organs and neural structures. In adulthood, T operates mainly through activational effects on mature tissues, such as maintaining sexual function and influencing cognitive processes (e.g., Christiansen, 1993). Administration of exogenous T, as might occur in the (ab)use of anabolic steroids, has been shown to increase strength and muscle mass in adult males when combined with exercise (Bhasin et al., 1996).

T follows a circadian rhythm, peaking early in the morning and declining about 50% over the course of the day (Dabbs, 1990b). Evidence exists that human males have circannual patterns of T secretion, but the reported peaks and nadirs are not consistent (e.g., Dabbs, 1990b; El-Migdadi, Nusier, & Bhashir, 2000; Maes et al., 1997). Seasonal fluctuations in reproductive hormones may be regulated by melatonin, the main hormone secreted nocturnally by the pineal gland. Reproductive organs have melatonin receptors, and there are receptors for sex hormones in the pineal gland, suggesting a relation between these processes (reviewed in Luboshitzky & Lavie, 1999) that could potentially account for discrepancies in reported circannual patterns of T secretion.

Males from a western population have been shown to have higher T than males from several non-western populations, with most of the differences occurring in younger men (Ellison et al., 1998). Interpopulational differences in T may be related to nutrition. Campbell and Leslie (1995) hypothesized that T production is constrained by the availability of energetic resources, which would prevent expensive muscle catabolism during a food shortage. However, evidence has not been forthcoming (Bribiescas, 1997) and male reproductive ecology suggests that since males do not provide any physiological investment after insemination, sexual or reproductive function should not be as sensitive to acute shortages of food, as has been demonstrated in women, whose reproductive hormone levels are known to directly fluctuate with energetic availability (Ellison et al., 1993). Weight loss and fasting, however, have been shown to suppress T in male wrestlers (Booth, Mazur, & Dabbs, 1993; Strauss, Lanese, & Malarkey, 1985).

T interacts with the immune system in meaningful ways. On average, T tends to compromise immune function, which could partially account for the higher rate of adverse health outcomes found in males relative to females (Campbell, Lukas, & Campbell, 2001). Secondary sexual characteristics brought about by T may represent indicators of immune system functioning during development (Grammer & Thornhill, 1994; Thornhill & Gangestad, 1996). Basal T levels are also somewhat heritable (Harris, Vernon, & Boomsma, 1998; Meilkle et al., 1987).

T has been linked to aggression in numerous species, although in humans the findings are equivocal (Albert, Walsh, & Jonik, 1994; Archer, 1991). Ehrenkranz et al. (1974) found that dominant but not aggressive prisoners had T levels nearly equal to those of aggressive prisoners (both dominant and aggressive prisoners had significantly higher T levels than prisoners rated non-dominant and non-aggressive). Booth and Mazur (1998) suggest that T is more accurately associated with dominance-related behavior in humans and is only implicated in aggressive actions when dominance is achieved through aggression. Possibly, humans have attained greater cerebral control over aggressive impulses than other species owing to our highly developed neo-cortex.

T has been positively associated with other characteristics such as heightened vigilance, more focused attention, more gregarious behavior, less paternal solicitude/nurturing behavior, and with "demonstrative occupations," such as trial lawyers and actors as opposed to tax lawyers or ministers (reviewed in Dabbs & Dabbs, 2000). Van Honk and colleagues have found that T is positively associated with increased attention to threatening male faces (1999) and that exogenous doses of T will increase cardiac response in women who are presented with pictures of angry faces (2001). The authors interpret these findings as suggestive of T's role in dominance behaviors and inclinations toward aggression.

Cortisol

Glucocorticoids (GCs) are a class of steroid hormones produced in the adrenal cortex and are critical for maintaining normal physiological function. GC production is continuous but increases markedly in response to physical and psychosocial stress. GC actions are complex and can have permissive, stimulatory, suppressive, or preparative effects (Sapolsky, Romero, & Munck, 2000). Areas affected by GCs include cardiovascular function, fluid volume and hemorrhage, immunity, inflammation, metabolism, neurobiology, and reproductive function. The major GCs are cortisol (C), aldosterone, and dehydroepiandrosterone (DHEA). Aldosterone acts on the kidney to conserve sodium ions from being excreted in the urine thereby regulating blood pressure. Little is known about the physiological activity of DHEA except that it is a weak androgen capable of being converted to estrogen (Norman & Litwack, 1997). C is the primary glucocorticoid in humans and has a very broad range of effects. C is known to modulate energy allocation, immune activity, mental activity, growth, and reproductive function. C secretion is regulated via the hypothalamic-pituitary-adrenal axis (HPA) (Figure 2.2).

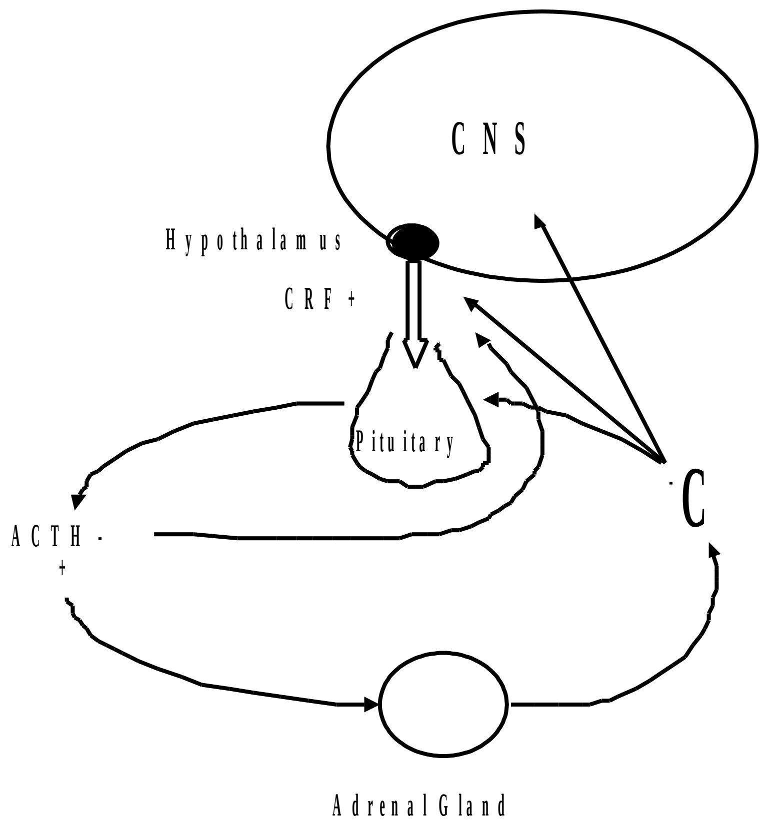

Figure 2.2 Hypothalamic-pituitary-adrenal axis.

C production increases in response to stress. External or internal stressors are perceived by the central nervous system (CNS), which signals the hypothalamus to secrete corticotropin-releasing factor (CRF) into the hypophyseal portal blood system, which triggers the pituitary to release ACTH (also known as corticotropin). ACTH travels through the circulatory system until it reaches the adrenal glands and triggers the release of C and other GCs. ACTH inhibits further release of CRF from the hypothalamus. C and other GCs have down regulating actions at the pituitary, hypothalamus, and CNS (Norman & Litwack, 1997: 350).

Most C circulates bound to corticosteroid-binding globulin (CBG) although a small amount exists in free form. Free C diffuses across cell membranes where it binds specific receptor molecules to form steroid-receptor complexes, which in turn bind chromatin in the nucleus to affect transcription and protein synthesis.

C production follows a diurnal rhythm, peaking in early morning before awakening and declining throughout the day. There is some evidence that this effect is not universal (e.g., Stone et al., 2001), indicating more research may be required.

The major metabolic function of C is to increase energy availability by stimulating gluconeogenesis, or the formation of carbohydrates. C liberates protein from muscle and fatty acids from adipose tissue, which are then converted to glucose by the liver and taken up and used by cells (Kaplan, 2000).

Increasing energy availability during stressful episodes is understandable. However, interpreting the effects of C on the immune system during times of stress is complicated. For instance, C has both stimulatory and inhibitory effects on immunity (Chrousos, 1995). Although considerable studies indicate that C reduces circulating leukocytes (white blood cells), a reinterpretation of these findings suggests that the body sequesters or redirects leukocytes from circulation to combat potential infection in peripheral tissues ((Dhabhar & McEwen, 1996). Immunity-enhancing effects of C through permissive effects have also been argued (Jefferies, 1991). Further complicating matters, the effects of GCs vary over the course of the stress response, with initial permissive actions giving way to suppressive actions (Sapolsky, Romero, & Munck, 2000). The evolutionary, or adaptive, rationale of C mediated effects on the immune system remain oblique at this point.

Other actions of C are more straightforward. As a powerful anti-inflammatory agent, C would, for example, allow prey to escape from a predator by preventing an injured area from becoming immobilized due to inflammation (Sapolsky, 1994). Other actions of C during stress-related episodes are inhibition of reproductive physiology and growth, and suppression of appetitive and digestive processes.

Acute stressors enhance memory formation, a process mediated by sympathetic release of catecholamines, which increase glucose delivery to the brain. The effects of C on memory formation are slower acting and operate through the hippocampus, a region of the brain critical for learning and memory. GCs increase delivery of oxygen and glucose to neural tissues involved in the formation of memories (McEwen & Sapolsky, 1995).

C production is stimulated by unpredictable and/or uncontrollable situations where it enhances mental acuity and alertness necessary for making decisions in these environments (Flinn, 1999; Kirschbaum & Hellhammer, 1994). C production is also stimulated by anticipation of stressful events, indicating that preparative actions of C are important, and that stressful events are often recursive and/or able to be cogitated ahead of time (Sapolsky, Romero, & Munck, 2000).

Long-term stressors that chronically elevate C levels are associated with a number of adverse health outcomes (Sapolsky, 1994) including depression. Short-term fluctuations in C levels appear to influence mood, or affect, although findings are not consistent. In general, C increases are associated with negative affect and a decrease in C is associated with positive affect (e.g. Smyth et al., 1998).

T/C Ratio

Discussion of the ratio of T to C (T/C) is relevant here because T and C affect each other reciprocally. In males, there is evidence that C inhibits T production (Cumming, Quigley, & Yen, 1983). In women this relation is more pronounced because T and C are mainly produced in the adrenal glands, whereas males largely produce T in the gonads. However, under competition conditions, males are capable of elevating both T and C simultaneously (Elias, 1981).

Given the known permissive effects of C, it is likely that C influences the effects of T, although details of this process are not well known. The metabolic effects of T and C are opposite; T is anabolic and C is catabolic. Some studies have found T/C ratio to be predictive of athletic performance such that a low ratio was associated with poorer performance (Mujika et al., 1996), although other studies have not found this effect (Hoogeveen & Zonderland, 1996; Vervoorn et al., 1992). There is also evidence that psychophysiological responses to stress vary with T/C ratio (Moya-Albiol et al., 2001).

Testosterone, Cortisol, and Competition

Non-human Primates

T and C levels fluctuate in response to dominance competition in a wide range of species, including primates. In the 1970s it was demonstrated that male rhesus (Rose, Holaday, & Bernstein, 1971; Rose, Bernstein, & Gordon, 1975), squirrel (Coe, Mendoza, & Levine, 1979; Mendoza et al., 1979), and talapoin (Eberhart & Keverne, 1979) monkeys elevate T in response to dominance challenges and that higher T levels are associated with a rise in status. Later studies have replicated these findings in other species such as baboons (Sapolsky, 1991).

C has been shown to increase in response to status competition in a number of primate species. Alberts et al. (1992) found increased C levels in baboons involved in dominance interactions with a newly immigrant male. Also, unstable primate groups as a whole have higher C compared to stable groups within and across taxa (reviewed in Bernstein et al., 1983). McGuire et al. (1986) reported increased C in adult male vervet monkeys that were competing for dominance, and Sapolsky (1992) found that C increased much more in baboons that were being challenged for their status position by any of the three closest lower-ranking males.

Rank may be an important modifier of hormone response to competition if individuals of different rank have different basal hormone levels, which in turn, affect their ability to elevate or decrease these levels during competition. For basal T levels, it is not certain whether correlations with status position exist. Sapolsky (1991) did not find a relation between T and rank in a stable baboon hierarchy, although recent evidence found that T levels were positively associated with rank in what appeared to be a stable chimpanzee group (Muller & Wrangham, 2001). These authors note however that small groups of males frequently disperse for long stretches of time and when these groups rejoin interactions are tense, as if dominance relations need to be reconfigured in light of any social maneuvering that has taken place during the interregnum. In this sense there may not be any such thing as a truly stable hierarchy among male chimpanzees (the authors note that they also may not have observed the group long enough for the hierarchy to stabilize). More evidence as well as a finer-grained analysis of what constitutes a stable hierarchy is needed.

C has a higher positive correlation with rank than T does, although McGuire et al. (1986) did not find such a correlation in stable-vervet-monkey-groups. Sapolsky (1990) did find that dominant male baboons in stable hierarchies had lower C levels. However, low C was later found not to be characteristic of all high-ranking males but only those that engaged predominantly in sexual consortships and grooming or were able to assess threats accurately—differences the authors attribute to "personality styles" (Ray & Sapolsky, 1992).

In the above studies, there appears to be some difficulty in ascertaining what constitutes a stable hierarchy. Part of the difficulty is that hierarchies are dynamic systems that continually change as individuals vie for status position, migrate, enter adulthood, grow old, and die. A consideration of rank is appropriate when examining T and C responses to competition, because as Sapolsky (1982, 1991) has demonstrated in baboons, high-status and low-status individuals have different hormone responses to stress—in this case being darted with anesthesia and briefly losing consciousness. For example, high-status males elevate C higher and faster than subordinates do, and they have initial increases in T in response to stress, whereas subordinates do not. However, even within this rank dichotomy there exist other behavioral or personality variables that influence hormone levels and responses to stress (Ray & Sapolsky, 1992). These factors may be important for understanding human hormone responses to competition because competition is a stressor, and as such, may elicit different hormone responses depending on personality or rank. Determining rank in humans, however, is difficult (discussed below). In broad terms, however, I adopt Mazur's (1985) model of primate dominance encounters, which is typified by (1) high or rising T in individuals who achieve dominance (2) low or decreasing T in those showing deference and (3) increased C in both competitors.

Humans

Studies of human hormone response to competition use ritualized contests and are largely consistent with Mazur's primate model. T and C levels typically increase slightly in anticipation of competition, and T remains elevated in winners relative to losers. Examining relations between rank and hormone levels in humans is problematic for a number of reasons: social status is difficult to ascertain and quantify; humans are not organized into obvious linear dominance hierarchies; and, particularly in industrialized populations, achieving high status is complex—for example, climbing a corporate ladder might require years of stressful maneuvering. One study, conducted on the same rural population of men used here, reported associations between high C and men: who had reputations for illicit social behavior; who reported frequent distressed moods; and who were rated by their peers as less trustworthy, agreeable, influential, and honest (Decker, 2000). These latter characteristics might be regarded as indicative of subordinate status.

Mazur and Lamb (1980) performed the seminal investigation into human hormone response by measuring plasma-T levels in males competing in doubles tennis matches. Winners received $100 each, and they found that winners experienced elevated T relative to losers except in one match where the outcome was decided on the final point. In that case, T declined slightly in all four contestants following the match. The authors also discovered that increased T was associated with an improvement in mood. Elias (1981) measured plasma levels of T, C, and testosterone-binding-globulin (TeBG) in collegiate wrestlers and found that T and C increased and TeBG decreased in all participants; that C increased more in winners; and that T remained elevated in winners relative to losers.

A team of Spanish researchers investigating hormone response in adolescent judo competitors (Salvador et al., 1987; Suay et al., 1999; Serrano et al., 2000) has not found the expected changes in T following outcome, although anticipatory surges in T and C were reported. The first study found that a contestant’s prior experience influenced his hormone response to the competition—more accomplished judoists had higher T levels. In a similar vein, Booth et al.'s (1989) monitoring of T levels for six members of a varsity tennis team during a season found that winning was associated with higher T before the start of the next match. Also, higher-seeded players had lower prematch C and all players trended toward lower prematch C levels as the season progressed. Improved mood was also positively associated with T.

Baerwald (n.d.) investigated T and C in competitive bicyclists with different levels of experience. He found that experienced cyclists had lower pre- and post-race C levels than did inexperienced cyclists. And, although T was not influenced by experience level, it was associated with a measure of perceived success. Baerwald also found that T/C ratio interacted significantly with a measure of trait anxiety, high ratios (more T, less C) associated with less anxiety and vice-versa. Intriguingly, pre-race T levels were positively correlated with the number of competitors.

To remove the possible confounding effect of exercise-induced hormonal increase (e.g., Kuoppasalmi et al., 1976), Gladue et al. (1989) examined T and C changes relative to a laboratory reaction-time task that did not involve physical exertion. Winners and losers were assigned randomly. T and C responses were significant, and T correlated with outcome in the expected directions, indicating that purely mental challenges induce competition-like hormone responses. Mood was positively correlated with T, as was attribution, a measure of how much the contestants felt they were responsible for the outcome. Thus, regardless of one's actual performance (remember that outcome was randomly assigned), the mere perception of winning or losing was found to affect subsequent T levels. European professional basketball players' perceptions about their contributions to the game were also found to correlate with post-game T levels, which also correlated with an objective indicator of their actual contribution—the ratio of points scored/time played. Post-game T levels were not, however, predicted by whether the team won or lost (Gonzalez-Bono et al., 1999). Serrano et al. (2000) also found T responses associated positively with self-appraisal of performance and attribution of outcome to personal effort. C response was consistently associated with negative mood.

Building on non-athletic competitive encounters, Mazur et al. (1992) measured T levels in males during a chess tournament and found that T increased just before matches and remained elevated in winners relative to losers. Interestingly, contestants with higher T levels in the morning of their match ended up winning. In one of the few studies to investigate female hormone response to competition, Mazur et al. (1997) conducted same-sex video-game competitions and found that T responses were different between the sexes but that C responses were similar. Whereas men's T increased before matches and in some cases across the match, women did not elevate T before matches and T decreased across matches in all cases. The authors speculated that T did not correlate with outcome in the men because the video game used was archaic by the player's standards and did not fully engage them—a conclusion they drew from the players' comments after the experiment.

The above studies indicate that T and C fluctuate in response to competition, but the direction of the responses may not be solely dependent on winning or losing (e.g. Serrano, 2000). It is likely that the significance of the competition to the individual is important for influencing hormone response. Also, mood may mediate T increase. Contextual factors may be important. In the Suay et al. (1999) study above, the authors noted that the competitions took place in a 'heat' environment consisting of many highly engaged spectators, although this did not stimulate significant differences in hormone responses between winners and losers. Contextual factors, such as audience size, are rarely incorporated into studies of endocrine response to competition.

Two exceptions are worth mentioning because they draw attention to the influence of others on hormone responses. Kirschbaum et al. (1995) found that men who received social support from an opposite-sex partner while anticipating a stressful event (public-speaking task) had lower C levels than men who received no support, although women showed the opposite pattern. Thorsteinsson et al. (1998) found that both men and women had lower C responses during a laboratory-based behavioral challenge when supplied with video-relayed social support from a same-sex confederate.

These studies underscore the importance of social context for hormone function in humans. To my knowledge, this is the first study in humans to explicitly address social context as a mediating factor of T response to competition. The context of male coalitions is hypothesized to be a meaningful factor owing to our unique evolutionary history of intense coalitional competition, explored below.

Significance of Coalitions for Human Evolution

> "You ain't shit without your homeboys."
>
> \- **Tupac Shakur**

Biological Significance of Cooperation

Ever since the first replicating entities appeared on earth (in whatever form) evolution has in many instances produced biological systems of increased complexity. One reason for this, of course, is that initially there would be only one direction for complexity to proceed (Gould, 1989). Greater complexity emerged when smaller replicating units combined forces to replicate as a larger unit. Branches of life that accomplished these tasks were awarded with untapped biological niches. The very first replicating entities eventually gave rise to simple cells. Simple cells, or bacteria, likely fused to form eukaryotic or complex cells (Margulis, 1981). Multiple complex cells then combined to give rise to multi-cellular life. Thereby creating the potential for cooperation among large, multicellular organisms. Cognitively sophisticated species, such as chimpanzees and cetaceans, engage in various levels of coordinated group competition (Connor, Smolker, & Richards, 1992; Goodall, 1986; Wrangham, 1999). However, large-scale cooperation in humans may represent a rather unique benchmark in the evolution of increasing organic complexity. Humans are the only species capable of coordinated competition in groups the size of millions, and the human brain is perhaps the most complex structure in the known universe.

Social Competition Hypothesis

Beginning in the late 1960s, biologist Richard Alexander has presented in a number of articles and books a codified model of human evolution depicting how intergroup competition among pre-humans was the key development leading to many features found uniquely in our species (Alexander & Tinkle, 1968; Alexander & Noonan, 1979; Alexander, 1974, 1979, 1987, 1989, 1990). His model synthesized findings from disparate fields that had not been previously brought to bear on human evolution (Geary & Flinn, 2001; Ward & Flinn, 2001) and provided a framework for analyzing humans from a biological viewpoint. Centrally, Alexander united Humphrey’s (1976) assessment of the brain as a social tool with balance-of-power scenarios that emphasize the contribution of group competition in bringing about larger, and necessarily more complex, social groups. Navigating increasingly large social arenas filled with equally sophisticated conspecifics would have provided the impetus for our rapid increase in social intelligence.

Living in large groups would have placed novel selective pressures on people of all ages. Primarily, competition for resources both within and between groups would have become more intense as group size and competition between groups increased. Concealed ovulation in females likely evolved to secure more paternal investment—males would need to continually remain with females to ensure paternal certainty (Alexander & Noonan, 1979). A primary function of paternal care was probably protection against infanticide by other males (Alexander, 1979). Increased parental care directed heavily sought after resources to altricial young who developed long learning periods for absorbing information about their social environments. Intimate knowledge of social environments was necessary for making correct decisions in complex social situations involving ego, family, friends, and enemies (Alexander, 1979).

Sophisticated cognitive mechanisms for detecting social cheaters (Cosmides, 1989), cooperation (Trivers, 1971), and possibly communication (Dunbar, 1997), can be seen as outgrowths of, or mechanisms for, living in complex social groups. Between-group competition selected for increased social complexity because cooperation entails complexity, and individuals who were better able to cooperate were more effective at intergroup competition. Humans became, in a meaningful sense, ecologically dominant such that other humans were the primary selective force and cooperating-to-compete became the primary selective pressure (Alexander, 1989).

Why this situation persisted to produce such extreme mental elaborations in humans is uncertain. Alexander (1990) points out that where selection is intense there will be many losers in addition to winners and wonders why humans who were on the verge of losing did not simply retreat from social competition. It must be true that in the line that led to humans, withdrawing from society would have resulted in even greater losses. Alexander suggests that humans became so dependent on the support of other humans that social retreat was no longer an option and cites as evidence the difficulty small extant human groups have in surviving. While this is accurate, it must be reconciled with the fact that some groups must have left to give rise to the numerous hominid species that have turned up in the fossil record. If Alexander's scenario is correct it stands to reason that these branching populations did not experience continued social competition, or at least not with the same force, as occurred in the lineage giving rise to modern humans. *Homo erectus* appears to have persisted in Java up until 26,000 thousand years ago (Swisher et al., 1996). Assuming cortical expansion in *Homo erectus* resulted from social competition, it appears that there is nothing inherent about social competition between groups that dictates they turn into cognitive arms races. In fact, the dearth of species engaging in this type of competition suggests that perhaps a unique factor, or a unique combination of factors, contributed to our particular evolutionary trajectory of intense social competition accompanied by rapid neo-cortical expansion (Alexander, 1990).

Unfortunately, the nature of these factors is not clear. Intriguingly, Cunnane et al. (1993) have drawn attention to the relation between brain constitution and essential fatty acids, which are abundant in marine ecosystems, suggesting that man's ancestors were extracting a significant amount of calories from marine-based food sources during cerebral expansion. If bodied water also militated against emigration, an island for example, a theoretical picture comes full circle: intergroup competition was driven into evermore-elaborate forms within a constrained environment where socio-cognitive advantages were underpinned by the availability of marine-based nutrients critical for cerebral growth. Though speculative, this scenario is consistent with rapid evolutionary change occurring in small populations associated with island environments (MacArthur & Wilson, 1967).

Regardless, it is undeniable that aggression-based-intergoup competition has been a prime mover throughout human history and likely pre-history (Keeley, 1996). As Robert Bigelow observed, “Five thousand years of savage warfare during historical times do not suggest a million years of prehistoric peace” (1969: 19). Ethnographic accounts of foraging societies are consistent with this view as well.

Case example: Yanomamo

Chagnon (1974; 1992) has provided intimate details of the lives of the Yanaomamo Indians of Venezuela and Brazil. His observations are considered indispensable for understanding ancestral patterns of human behavior because the Yanomamo are largely unfettered by modern contact, although unfortunately this situation is changing much to the detriment of the tribes. The Yanomamo consist of roughly 20,000 individuals living in some 200 villages interspersed throughout the dense Amazonian rain forest. Endemic conflict between villages is the most striking feature of Yanomamo life. Disputes between individuals or communities are sometimes mediated through chest-pounding duels, in which each man takes turns striking the other in the chest with the ball of his fist until one side concedes. Occasionally, duels escalate and can result in more serious injury, for example, when long poles, normally used to support housing structures, are used to strike instead of fists. Men frequently conduct group raids on other villages in which they attempt to kill men for retribution or, ideally, capture women. Chagnon reported one instance in which a village invited a neighboring group for a feast under good pretenses, only to turn savagely on them upon being given a pre-arranged signal (1992).

The Yanomamo are a fission-fusion society. Villages average about 75–80 people and are organized around two and rarely three paternal lines. Villages tend to fission when they reach 150 individuals, splitting along lines of male kinship, and lower limits on village size are constrained by the need to have enough adult males (10–15) to engage successfully in inter-village conflict. Small villages are forced to unite if they are to survive, or join a larger group although this usually results in disadvantages for the smaller group and particularly the men. Chagnon has reported that successful warriors, those who have killed other men, have higher reproductive fitness than men who have not (1988).

Relation Between Social Competition and Hormone Mechanisms

In many primate species, such as baboons and chimpanzees, males will cooperate in small coalitions as they attempt to increase their position in the dominance hierarchy. Increasing dominance generally translates into reproductive benefits (see Ellis, 1995, for a cross species review). In baboons though, coalitions are fleeting as Sapolsky's description of male baboon coalitions exemplifies, "Forming a cooperative coalition with another male can be very helpful in a fight; however, when the fight actually occurs, the male often fails to aid his coalitional partner, or even defects to the opposing side" (Sapolsky, 1991: 282). In contrast to most primates with the possible exception of chimpanzees, in humans male bonding is pervasive. In the lineage leading to humans, coalitions of males began to weaken the reproductive abilities of males either not allied in coalitions, or in relatively weak coalitions. Male reproductive success was still being sorted through status competition and coalition building within groups, but the integrity or cooperative abilities of these coalitions was now relevant within a larger sphere of male coalitions. These coalitions, built around male kin, engaged in various fitness enhancing and debilitating behaviors in connection with other coalitions. Competition for mates, and also for feeding and watering sites, were likely carried out through coalitional raids, to capture women and weaken other male coalitions through killing (Chagnon, 1992; Manson & Wrangham, 1991; Wrangham, 1999).

Being a part of a larger and/or more effective coalition has obvious advantages in these situations and, although offset by increased competition for resources within groups, was carried to an extreme in the human lineage. As such, the ability to cooperate with other males for purposes of intergroup competition became paramount and produced significant changes in the dynamics of male competition. Male reproductive success would have become increasingly dependent on securing allies through the cooperation of other males, rather than simply dominating them.

Competition among human groups fostered cooperative male coalitions, which may have required a limit on overt dominance strivings that might otherwise weaken a coalition. Efforts to increase social status through dominating other males, at least within small-scale societies, are typically regulated by other group members through various leveling mechanisms (Boehm, 1993; 1999). As such, expressing dominant behaviors or becoming overly aroused (indexed by T and C levels respectively) during within-group dominance competition may have been a liability for males who would then be subject to leveling by other coalition members. Also, excessively dominated individuals would be more apt to vote with their feet, or abandon their group, thereby jeopardizing the fitness of the other members.

As Boehm states, “From a dominant individual’s reproductive success, the ability to cope collectively with predators or with competing conspecific groups is improved if overdominated subordinates are not driven away. From the subordinates reproductive perspective, it is better to live in groups—but not be dominated so severely” (Boehm, 1999: 125–6).

The emergence of extensive coalitionary competition, thereby, generated two qualitatively different arenas of social competition—within and between groups—that would have required different competitive and/or cooperative mechanisms to negotiate effectively (Geary & Flinn, in press). As we have seen, hormone levels influence cognition and behavior and it is likely that mechanisms for cooperation and competition are similarly influenced. T mediates dominance related behaviors and T response to competition is therefore likely to be relevant for measuring dominance displays. C level is generally indicative of an organism’s state of arousal and increases in uncertain social situations. Therefore, expressing dominant behaviors or becoming overly aroused (indexed by T and C levels respectively) during within-group dominance competition may have been militated against, especially for males who would be subject to leveling by other coalition members.

When competition occurs between distinct groups or coalitions however, the opposite pattern should obtain. Now, flooding the system with T and C, at least during the initial stages of competition, would be highly beneficial. Further, if being a member of a stable and influential coalition is associated with lower basal T and C levels in general, then any increase in these hormones will have greater effect. Broadly, male-coalitions may resemble individual baboons in terms of status, hormone levels, and the ability to elevate hormones in response to competition.

The advent of larger coalitions (tribal alliances, chiefdoms, states) necessitated centralized authority figures (Service, 1975) that could better organize more expansive operations. In these contexts, which occurred more recently, individual striving for high-status may be tolerated and within-group restrictions on dominance behaviors will be less severe. Anecdotal evidence suggests that leveling mechanisms are prominent in the study population (A.L. personal communication). It is possible that living in stable, kin-based, egalitarian communities could contribute to lower T levels reported in non-western males (Ellison et al., 1998).

Research question and predictions

The objective of this study is to determine whether the context of male coalitions (within or between) influences hormone response to competition. It is predicted that dominance behaviors in humans have become highly regulated and as such hormone response will be lower during within-coalition competition relative to between-coalition competition. Or conversely, that between-coalition competition will stimulate greater hormone release relative to within-coalition competition. Both hormone levels and changes across the match are predicted to be greater during competition against an outside coalition as opposed to competing within one's own coalition. T/C ratio is also explored.

Chapter Three: Field Site, Village of Bwa Mawego, Commonwealth of Dominica

Dominica

The Commonwealth of Dominica, or simply Dominica, is a rugged volcanic island located in the Caribbean Sea about midway between Puerto Rico and Trinidad along the inner arc of the Lesser Antilles (Information for this section is drawn from "The Dominica Story: A History of the Island," by Honychurch, 1995, unless otherwise noted). Guadaloupe is to the north and Martinique to the south. At 29 miles long and 16 miles wide, Dominica is the largest of the Windward Islands and its 300 square miles belie its true area because of its mountainous topography.

During the Miocene period (26–5mya) Dominica formed along the fault line between the Caribbean and Atlantic tectonic plates. These plates are being pushed against one another, with the Atlantic plate being subducted, or pushed under, the Caribbean plate. As this happens, the crust from the Atlantic plate becomes heated by the earth's core, decreasing its density. The resulting magma then wells up and breaks through the thin Caribbean plate above, giving rise to a volcanic island.

The Lesser Antilles consists of an inner and an outer arc. The outer, eastern, arc is older, and has been leveled by the forces of erosion. Dominica, as part of the younger, more recent inner arc, has not been subjected to much leveling. But even so, Dominica stands as an anomaly among its neighbors because of its extreme relief. Morne Diablotin, at 4747 feet, is the highest point on the island and dominates its northern half. Four other mountains rise over 4000 feet, and a chain of seven mountains extends from the island's center to the south.

The topography is marked by a large number of ridges and deep, narrow river valleys. Flatter areas are restricted to the coastal areas of the northeast and center of the island.

Dominica’s weather is characterized by little seasonal variation in temperatures and strong, steady northeast trade winds. The island is the wettest in the Caribbean, with rainfall reaching in excess of 400 inches per year in the upper mountains. The seasonality of rainfall gives two seasons: a dry season in the winter months (December and January are the driest), and a rainy season during the summer months, with June and July being the wettest. The high mountains in the east absorb much of the rainfall from the prevailing trade winds, leaving the flatter, western side of island comparatively drier.

Known as "The Nature Island of the Caribbean," Dominica is home to innumerable rivers and streams. Waterfalls, fumarole areas, a boiling lake (considered the world's largest) and four cold freshwater lakes (two are over 2500 feet in elevation) are other natural attractions on the island. A standard joke is that Antigua (a nearby island) is home to 365 beaches, while Dominica is home to 365 streams. The rich volcanic soil, heavy rainfall, and rugged terrain conspire to resist development and make Dominica one of the most lush locales in the world.

Native Americans traveling from South America may have reached Dominica as early as 3100 B.C. Arawak Indians settled the island prior to European discovery but appear to have incurred an invasion from another South American group that has entered history as the "Caribs," although they are correctly identified as the Kalinago. As a result of its rugged terrain, Dominica provided a refuge for native peoples during the onslaught of European colonization. To this day Kalinago descendants live on the Carib Reserve, located on the east-central coast.

Discovered and christened by Christopher Columbus in 1493, Dominica did not absorb its first European inhabitants until the early seventeenth century in the form of missionaries. A steady stream of European colonists followed, mainly French lumbermen, and by 1727 about sixty French families made their homes on the island along with a handful of English Catholics, Spaniards, and Portuguese. A number of African slaves arrived shortly after. Nearly all imported slaves were sold to wealthy owners on lucrative sugar islands such as Barbados, Antigua, and Guadaloupe, and only came to Dominica indirectly. Nonetheless, by 1745 the non-Carib population stood at roughly 3000, over half of who were African.

Control of the island oscillated between Britain and France throughout the seventeenth, eighteenth, and early nineteenth centuries. Britain sought control of Dominica for strategic purposes because it was situated between the French colonies of Martinique and Guadaloupe. Dominica became a British colony in 1783 (which it would remain until 1978), although the French still controlled the island intermittently up until 1805. In spite of its British heritage, Dominica is most heavily influenced by French culture, likely the result of the early settlers, who passed on their lifeways through the generations. This is reflected in the languages of the island. Although English remains the official language, many islanders, particularly in rural areas, communicate among themselves in French patois.

The estates and peasant farms that were established during the eighteenth and nineteenth centuries brought large numbers of Africans to Dominica. Important crops at this time included coffee, cocoa, and sugarcane. However, the topography of Dominica militated against large-scale agricultural operations, and the estates that were established never approached the dimensions of those on the other Caribbean isles. The topography did, however, provide an excellent refuge for escaped slaves throughout the colonial period, just as it did for the Kalinago during European encroachment. Early escaped slaves intermingled with the Kalinago, who still survived on the isolated cliffs of the East Coast, and learned survival skills for living in the bush.

An increasing population of escaped slaves contributed to the establishment of chiefdoms in the rugged interior. These inhabitants became known as Maroons because of *marronage*, a practice in which escaped slaves returned to plunder plantations and rob citizenry. Marronage increased during times of British rule because slaves received harsher treatment from British, relative to French, slave owners. Maroon and French forces would even cooperate to raid British controlled plantations (Baker, 1994: 74–76). A series of skirmishes with European authorities at the beginning of the nineteenth century, however, brought marronage, and maroon way of life, to an end.

Although the rebellion was crushed, prevailing sentiments had changed. Emancipation of the slaves occurred in 1834, and with it the plantation-based economic system fell apart. The populace fractured into numerous horticultural villages, which would form the basis of Dominica's independent peasant society—an arrangement still very much in effect today.

Dominica's economy is based on agriculture, and many rural islanders rely on subsistence gardening for their livings. Cash crops have always provided laborers and small-scale farmers with a means of procuring market goods. Cocoa, coffee, coconuts, sugarcane, limes, copra (dried coconut meat from which oil is extracted), and vanilla have been historically important cash crops whose ubiquity fluctuated according to external market conditions as well as internal class struggles (see Trouillot, 1988: 51–65). Bananas have been Dominica’s leading export commodity since the early 1950s, when a trade agreement was reached between a state agency (a cooperative) and a British-based multinational corporation that delivers the produce for sale in Europe (Trouillot, 1988: 32). The cooperative fixes prices for growers but also guarantees the growers a market for their goods. World Trade Organization and U.S. decisions concerning free trade have challenged these trade agreements in recent years.

Another important cash crop is bay-leaf oil, made from the bay leaves that grow abundantly throughout the island. Oil is sold to a cooperative, which again fixes prices and therefore the amount of cash that growers receive. The bay oil is then resold to manufacturers for use in soaps, lotions, and tonics.

With a population of 71,540 (July 2000 estimate), Dominica remains the least densely populated island in the Caribbean. As a result of its steep, mountainous terrain, nearly 67% of the island remains under forest and woodland. The annual growth rate of —1.26% (1997 est.) is mainly attributed to the migration of young people who seek fortunes elsewhere (Net migration = -24.04/1,000 population, 1997 est.). The capital, Roseau, is located on the southwest coast and has a population of 10,000. Dominica retains a British style parliamentary government, with a number of political parties continually vying for control. The dominant religion is Roman Catholic (77%), followed by Protestant (15%). Literacy, defined as over the age 15 and having attended school, was estimated at 94% in 1970.

Village of Bwa Mawego

Geography and General Information

Bwa Mawego is located at the end of a coastal-hugging road on the eastern coast of Dominica. The road leading to Bwa Mawego was once connected to a continuous loop encircling the island. But a portion of the road to the south of Bwa Mawego was washed away by a hurricane in the 1950s and has not been replaced. As a result, the village remains somewhat isolated from the rest of the island.

Bwa Mawego occupies the interior and coastal regions between two north-south promontories. Roughly 800 inhabitants make their homes along the road and numerous trails that trickle toward the coastline (Dubrow, 1993; R. Quinlan, 2000). The number of villagers fluctuates throughout the year as people come and go for school, work, and extended visits with kin. A steady decrease in population, most likely a result of emigration, has been observed over the past 20 years (R. Quinlan, 2000).

Housing and Services

Most villagers live in small (one to several room) houses with two side buildings, a kitchen and a latrine. Older houses were constructed of wood, but newer ones are constructed of cement blocks. Corrugated metal roofing is now ubiquitous and is often used to channel rainwater into catch basins for washing, cooking, and drinking. Water can also be collected from the numerous streams (some with standpipes) that run through the village. These water sources also double for bathing and washing.

As is often the case in the industrialized world, housing disparities are noticeable in Bwa Mawego. Some homes have now acquired indoor plumbing and latrines and are replete with modern appliances, whereas others appear as uninhabitable, rotting shacks. Most houses have wooden shutters for windows, although one building under construction in summer 2000 was equipped with modern glass windows.

The rugged eastern periphery of the island has contributed to a relatively underdeveloped infrastructure in Bwa Mawego, although this is steadily changing. Electricity arrived in 1979, but Hurricane David promptly destroyed the power lines. Service was not restored until 1987, but today roughly 80% of households have electricity, which is primarily used for lighting and radios. Modern appliances such as TVs and washing machines are few but are becoming increasingly more common. About half of the village still cooks over an open fire, while the other half rely on small propane stoves.

Transportation to and from Bwa Mawego is difficult. A half-hour ride by car separates the village from the main road, where taxis and buses run regularly. One young man communicated this difficulty to me. He and a group of friends were planning a Sunday trip to the beaches on the northeast coast. He explained that a "transport," usually a minivan that can hold a maximum of 20 people, had to be arranged for several days in advance to pick travelers up in the morning and to return them in the evening. The cost to individual riders was between $8 and $12 E.C. depending on the number of travelers—a considerable sum to most young people in the village. Through the week, transportation is available at dawn. Two or three transports make a daily roundtrip to the capital for $9 E.C. per person each way. A round trip takes four hours and is not a smooth affair. Hairpin turns on narrow hilly roads riddled with potholes are the norm.

Although Dominica has socialized medicine, it is difficult for villagers to access healthcare because of transportation constraints. With no medical facilities in the village and the nearest pharmacy and hospital two hours away, villagers often have to rely on home remedies made from local plants and herbs (M. Quinlan, 2000). However, a nearby clinic does provide limited medication, immunization, first aid and various check-up services. A recent fire caused the clinic to temporarily relocate inside the village.

Education begins at the infant school located in Bwa Mawego for children between the ages of five and seven. The school is staffed by local women and has sessions until noon through the week (M-F). The government provides some financial support for primary education, although schools are sparse. Fortunately, a government-funded primary school is near Bwa Mawego. Upon completion of primary school, around age 12, a “common entrance exam” is given which determines who will attend one of the few secondary schools on the island. The ability to attend secondary school is dependent not only upon the student’s test scores, but also on their family’s ability to pay for textbooks, room, and board, which can be quite expensive. Competition is stiff, but students who are able to attend secondary school increase their chances to land coveted government jobs, or attend a university off the island. Attaining this level of education is very rare for most villagers, however.

Goods and Economy

The majority of villagers grow some portion of their food in gardens near their homes. Dasheen, yams, plantains, taro, coconut, breadfruit, mangoes, pumpkin, cucumbers, breadfruit, and papaya are some of the many foodstuffs that islanders cultivate, or are available seasonally. Increasingly, villagers are becoming accustomed to imported items, and particularly starches such as beans, rice, pasta, and flour. The increasing popularity of these items may stem from the fact that cultivating yams and other root species requires arduous labor.

Fish, pork, chicken, and goat provide dietary protein. Game is usually hacked into equal size pieces (with bone and skin attached) then boiled with other vegetables and fruits to create stew. Fresh fish is often available daily and is prepared much the same way. Frozen chicken imported from the United States, once a scarcity (Decker, 1993), is now commonplace.

Eggs, canned meats, powdered milk, coffee, cigarettes, beer, soap and other consumer goods are available from a handful of shops in the village. Other commercially produced goods, such as clothes, shoes, and appliances, require trips to larger stores located in the bigger villages or town. Compact discs, stereos, and other electronic devices are quite a bit more expensive than in the United States.

The range of economic opportunities is limited. Cultivating bananas and bay-leaf oil are the most common and potentially lucrative occupations, but require enormous inputs of labor. Driving a transport, working in town, running a shop, carpentry, teaching school, gardening, fishing, and construction are other employment options. During my stay, construction work was readily available since an apartment building and a government building were being built nearby. Most construction jobs, however, are distantly located and require extended stays away from the village. Many men have worked as migrant laborers in Canada and the United States. While these jobs provide an opportunity for the men to earn more money than they could otherwise, they also require long stretches of time away from friends and family. A few villagers have also worked at hotel resorts on neighboring islands; one man in the study had briefly worked in Antigua as a luggage porter. Occasionally women find employment as domestic servants in town or on other islands. During my visit, several women from the village worked in town at a flower shop and a travel office.

Banana production has declined in Bwa Mawego in recent years because cooperatives are able to offer better prices for bay-leaf oil. Bananas also require meticulous attention to detail by the growers in order to be accepted by the cooperatives. This arrangement is the result of a series of increasingly stringent guidelines for banana quality that have unduly placed much of the burden for growing bananas onto the growers.

Although lucrative, producing bay-leaf oil is extremely demanding. The first phase involves cutting the leaves from the bay leaf bushes, which grow on steep slopes around Bwa Mawego. The leaves are bundled into 90-100 lbs. bails that are carried over slippery mountain paths to one of seven distillation factories in the village. The biting ants that live in the bushes contribute to the discomfort of this process, which can take up to a week or longer.

An enormous amount of firewood must also be cut, carried, and dried, to keep the distillation process—which can take up to four days—running. Roughly one bail of bay leaf (~100lbs.) is consumed every hour and produces the equivalent of about $40 E.C. A four-day distillation effort can generate upwards of $3500 E.C., a substantial sum in the village economy. Distilleries and bay-leaf plots are owned but can be rented out by their owners to various groups of laborers. Bay oil production is often a family affair, with the plots and factory owned by a single family who also provides the majority of the labor.

For several village men, fishing is a full-time occupation much of the year. They own their own small fishing boats and sell their catch to locals. Dolphin, shark, white fish, and balao are common species. A dearth of convenient docking sites limits the number of crafts (there are fewer than a dozen) as well as the number of fishermen.

Recreation

Residents of Bwa Mawego maintain an active social life. In the early evenings after work, villagers convene at one of several flat, natural gathering spots in the village. Workers returning from the fields and commuters returning from town intermingle easily as people of all ages exchange stories, gossip, barter, and generally revel as the daylight hours come to a close. Lying close to the equator, there is not much variation in day length and it is usually dark by eight in the evening. Electric lighting has allowed these gatherings to continue into the night, and villagers are often found at one of the nearby shops, which also function as bars. Rum followed by a water chaser is the traditional drink of choice, although beer is increasingly becoming a standard—with imports such as Guinness and Heineken competing with the locally produced Kubuli lager. Men, and occasionally women, frequently play dominoes at shops during the evenings.

As in most communities, sports are an integral part of young peoples' lives. Major sports for boys and young men are cricket and soccer, while girls play a version of cricket called "rounders." The village supports two cricket teams that compete with other villages. The cricket field lies close to the shore and is one of the few level-playing surfaces in the village. Even so, the periphery of the field is marked with abrupt bunkers and precipitous drop-offs. It is not uncommon for a player to scamper down a craggy slope after an errant hit.

Dances are another popular social outlet for young people. A rather impressive dance club sits near the top of the village and attracts people from all over the island. A nominal cover charge grants one access into a dimly lit world of pulsating techno music that persists until the wee of hours of the night.

The ocean is also a popular gathering spot. Negotiating the rugged, rock-strewn shoreline can be challenging, particularly when large waves pound the coast—sometimes with spectacular effect. Groups of young men will often wile away the daylight hours by the sea swimming, sunning, spear fishing, hanging out, joking, and making up games of skill. Breadfruit cooked on an open fire and seasoned with spiced butter provides sustenance. A few fish might compliment the meal provided a skilled hunter is in attendance.

Visiting neighbors, relatives and friends are common activities for all villagers. Several major holidays are ritually observed: Carnival marks the beginning of lent; the feast of the village patron takes place in mid-summer; August Monday (Independence Day), and the Yuletide. All are occasions for gathering and celebration.

Chapter Four: Methods

This chapter reviews participant selection; describes the history of dominoes and their role in village life; presents the study design and an overview of the matches; and describes techniques used in saliva collection and analysis.

Participant Selection

Fieldwork was conducted over two weeks in the village of Bwa Mawego. The ethnographic techniques of participant observation and key informant interview were used to select participants. Participant observation involves casually interacting with members of a community in ways that make sense to them (Bernard, 1995: 136–164). The goal is to limit subject reactivity to the investigator. I strove to blend in with the men and hang out on their terms (which, on one occasion, consisted of drinking rum until the wee hours of the morning). I was fortunate to arrive on a weekend because a social gathering that evening allowed me to begin assessing the men's social network immediately through observation.

Participant observation encourages rapport, and I established especially good rapport with several men who I would also enlist as key informants (Chagnon, 1974). One man in particular, A.L., was invaluable as a source of information, an assistant, a participant, and a friend. Information passed to me from key informants was essential for quickly identifying suitable participants for the study and for learning the status of their relationships with each other. I also benefited from having made acquaintances during an earlier trip to the village, and from the fact that previous investigators have established good relationships with the villagers (e.g., Mark Flinn, Rob and Marsha Quinlan, Seamus Decker, and Dave Leone), which, in my opinion, greatly expedited the research objectives.

Using the ethnographic techniques above, I was able to recruit closely bonded men who would provide compelling social interactions. Although I cannot be certain that the men chosen constituted a natural coalition, every source of information to which I had access indicated this was the case. The more tightly bonded the coalition, the greater the contrast should be when it came to competing against outside coalitions—allowing me to test the effect of coalitional context on hormone response to competition.

Additionally, I wanted to avoid recruiting men who were motivated to participate because of the money involved. Although I wanted strong reactions to winning or losing, it was more important that the men react to the social dynamics of the situation and not simply to whether they missed out on, or were elated to come into, a small sum of money.

Age was another consideration and I focused on adult men in their twenties for two reasons: T levels are high at these ages on average (Dabbs, 1990a), and men also predominantly engage in conflict at this age (Chagnon, 1992; Daly & Wilson, 1988; Wrangham & Peterson, 1997). Eight men between the ages of 19 and 36 (mean = 23) were selected based on their social relationships—all were well acquainted with one anξother including two brothers and two cousins. All men were in good health and were experienced domino players.

I would also like to note that while the ethnographic techniques used here were valuable, more importantly perhaps was the overall friendliness of the villagers. One might expect a closely-knit community to be suspicious of outsiders. However, the people of Bwa

Mawego have a social charm that instantly puts one at ease. Perhaps borne from a lifetime of daily interaction with parents, siblings, cousins, friends, grandparents, neighbors, and people of all ages—interactions that are increasingly unfamiliar to us today—the social graces and amiability of these people are truly astounding. The men who participated in the study were exceedingly tolerant, generous, dependable, and gracefully accepted their experimenter's assuredly bizarre requests.

What is Domino?

Dominoes are small tiles traditionally carved from ivory or bone with small, round pips, or spots, of inset ebony and are used to play a wide variety of games (Information for this section is drawn from "The Rules of the Game: Dominoes," by Grady & Goldberg, 1995). "Domino" is French for a black and white hood worn by Christian priests, and this is probably where the game takes its name. However, domino is clearly an eastern invention. The first domino sets date to 1120 A.D. from China and were derived from cubic dice likely imported from India. Interestingly, American Inuit people play a game using domino-style tiles suggesting the game might predate the last eastern migration from Asia into the Americas. Clearly, domino has a very ancient origin.

Domino didn't make an appearance in Europe until the early eighteenth century, which is surprising because the silk trade route had by then been long established. Domino first appeared in Italy at the courts of Venice and Naples before spreading to France and then Britain by the late-eighteenth century. French, British and possibly Portuguese colonialists took the game with them to the New World. Today, domino is played in almost every country of the world, being most popular in Latin America.

The form of domino that made its way to the Caribbean, via Europe, consists of 28 tiles. Each tile is representative of a unique throw of two dice plus a blank. This is called a standard or “double-six” set. There are seven pieces of each “suit”—a blank suit plus one through six. Each tile has two values, one on each end, indicated by the number of pips (or none in the case of blanks). Each suit has a “double-piece” that has the same value on both ends.

Domino can be played with two to four players, but the most popular and common method is to play with four players in two teams of two. The dominoes are mixed up face down on the table and each player selects seven tiles. The double-six piece begins the match and play proceeds in a clock-wise direction. Matching the values on the ends of the tiles plays a domino.

The objective is to be the first player (or on the team of the first player) to play all of their dominoes. Teams strategize by trying to figure out what tiles their partner is holding and what tiles the opponent is holding. In this way, players attempt to block the other team from being able to play their dominoes. The number of points awarded to the winning team at the end of a round is equal to the number of pips the losing team is left holding.

Role of Domino in Bwa Mawego

Domino is an integral part of life in Bwa Mawego, accompanying nearly every social gathering. Boys grow up playing the game, and domino sets can be found in most homes. Men often play long into the night, and matches can become quite animated; disputes are not uncommon. Games are usually quite competitive, especially when wagering is involved.

About every other weekend, a match takes place between Bwa Mawego and another village. For an away match, roughly 15–25 men will make the trip, but of these only about eight will actually play, with players taking turns. Matches last much of the day. Although the victors' spoils are relatively minimal—a case of beer paid for by the losers—locals have assured me that the outcomes of the matches are important to village morale. The village matches seem to be an activity reserved for elders in the village. During my stay, one such match occurred, although none of the men in this sample participated.

As in any game where sharing information between team members is advantageous, nonverbal communication is at a premium. For domino, the manner in which a tile is played is the most striking communicative gesture of the game. Pieces are frequently slammed down with table-jarring authority, while others might be played more softly. Upon playing the last, or winning, domino a characteristic shout of "do!" (short for domino) typically accompanies a demonstrative "thump" of that tile on the table. As a novice, I originally interpreted a thumped domino to mean a player was signaling to his partner that he was strong in that particular suit. A more softly played domino might then indicate reluctance on that player's part in playing that piece. In some instances this was surely the case, but with time I sensed that this was not always so. I eventually detected a great deal of bluff and miscommunication. At times, players seemed to be thumping their dominoes in an attempt to fluster their opponents, perhaps pressuring them into a bad move. This seemed especially true once I noticed that there was an emphasis on playing quickly; players who hesitated and took longer to play were generally chastised. These realizations increased my confidence that domino matches provided meaningful dominance-related interactions and could serve as a useful medium for simulating dominance competition.

Study Design

Domino matches were held over three consecutive days. On the first day, the men competed in the village among themselves in two simultaneous matches held during the early afternoon. On the second day, four of these men traveled with me to the next closest village and two matches were held in succession against local men there. However, these matches are excluded from this analysis for two reasons. One, the matches did not take place at the same time as the previous day. Significant rainfall prevented us from arriving at the village promptly, and the matches did not take place until the early evening. Because hormone levels are known to decline across the day (Dabbs 1990b), this prevented meaningful analysis, although adjusting for daily hormone clines is possible. However, the second and more serious concern was that one of the men in the original sample was technically a resident of this next village, living just outside the border of Bwa Mawego. It became obvious that he was familiar to and closely affiliated with men from this neighboring village, thereby blurring any distinction between the groups. In hindsight, the villages probably were too closely connected to test for within- and between-coalition effects on hormone response. On the third day, four men—two from the second day plus two others from the original sample—traveled to the distant village of "Le Maine" (a pseudonym) and competed against men from that village.

I originally anticipated using all eight subjects for the away matches but was concerned that there would not be enough equipment (tables, chairs, dominoes) in the other villages to hold the matches simultaneously. This was of special concern because the number of matches for the between-coalition condition is twice that of the within-coalition condition—there are twice as many competitors. As it turned out, it was not even possible to arrange for two matches to be held simultaneously at the other villages. This resulted in some methodological difficulty discussed in the next chapter. It also became apparent on the first day that collecting saliva from eight men while also monitoring two matches at the same time was difficult. For these reasons, groups of four, rather than of eight, participated in the between-coalition matches.

Status Ratings

As part of a related research project, I collected information on social status for 65 village men between the ages of 18 and 52. Six of the eight men who participated in the domino matches were included in this sample, including all four who participated in both conditions. Status ratings may have some relevance for understanding hormone responses to competition and are discussed in chapters five and six.

Twenty interviews were conducted in which I asked male informants to rate the men (shown as pictures) based on how much respect they received from people in the village. Ratings were given as percentages and most informants were in the sample, but did not rate themselves. About half of the informants immediately understood what was being asked but if they hesitated or looked unsure, I continued,

> "Use your own opinion but also think about the village as a whole and rate the men based on how much respect you think they receive from the whole village. That is, how much do other people listen to what they have to say, seek them out for advice, and take their opinions seriously. If you think they get a lot of respect, give them a higher percentage, if you think they don't get that much respect, then give them a lower percentage."

One early informant expressed instant enlightenment, "oh, you mean how he moves." It emerged that the way a guy "moves" is synonymous with how much "respect" they were accorded. For instance, one early informant gave this description of a man whom he rated highly:

> "He doesn't say much you know, I mean, I don't really talk to him that much. But that's okay because people know he is a good guy, they can trust him. He's not going to start any trouble or anything like that. Yeah, I would say I like the way this guy moves, you know handles himself, just going about his business."

Thus, I would occasionally expand on the meaning of respect, as in, "you know, the way he moves." Interviews lasted about twenty minutes and informants were paid $5 E.C. for their efforts.

Saliva Collection Techniques and Assay Procedure

Techniques for measuring hormones through saliva were developed in the late 1980s and have been a boon for researchers interested in studying human endocrine function in naturalistic settings (Ellison, 1988). The discovery that free hormone diffuses through salivary gland tissue led researchers to modify previous methods for assaying plasma hormones in order to measure the much lower free hormone concentrations present in saliva (Blood levels of hormone are about 10–20 times higher than saliva levels). Both T and C saliva concentrations are highly correlated with plasma levels (Wang et al., 1981; Vining et al., 1983).

The protocol for collecting saliva in this study was as follows. Participants were first asked if they had recently drank or eaten anything, and if they had experienced any bleeding in their gums. If they had, they were asked to rinse their mouths out with water because food and blood contamination can affect the integrity of samples (Ellison, 1988). Participants were then given one-half stick of Wrigley's gum to stimulate saliva production and asked to expiate 10ml into a plastic cup, which typically took 2–3 minutes. At this point, saliva was checked for a pinkish tint indicating it was contaminated with blood. This happened on one occasion and the man was asked to rinse his mouth and expiate again. His saliva appeared clear at this point although this sample would not ultimately be used as it was collected during the second day's matches, which were excluded from the analyses. About 4ml of saliva was then pipetted into labeled (name, date, time, number) polysterene test tube containing the preservative sodium azide (Flinn & England, 1997). This protocol was performed one-half hour before the start of the matches and then repeated (except for the questioning) immediately before the match and then twice after the match ended. Following the conclusion of the match, roughly 15 minutes were allowed to elapse before collection of saliva began to allow for serum hormone levels to equilibrate with salivary hormone levels (Read, 1993), or, in other words, for hormone changes to be detected in saliva. An additional sample was collected at 45 minutes postmatch. Samples were frozen within several hours of collection and remained frozen until assays were performed. Saliva can be kept at room temperature for at least two weeks without affecting T measurements in men (Dabbs, 1991).

Samples were assayed at University of Michigan Hospitals, under the supervision of Dr. Barry England. The ACS-180 hormone assay, which uses an antibody directed against a serum hormone albumin conjugate, has been modified to measure the low levels of free hormone found in saliva. This assay method is based on the competition between T or C and a dimethyl-acridinuim ester (DMAE)-labeled derivative for binding sites on a rabbit polyclonal anti-hormone antibody. The standards were diluted and the volume of sample used was increased in order to increase the sensitivity of the assay.

A brief description of the instrument procedure follows. A total of 200 microliters of the standard/sample antibody mix was collected by the sample probe and added to the on-board incubation cuvette. Hormone labeled with DMAE, and mouse anti-rabbit IgG (ARGG) conjugated to paramagnetic particles (PMP), were added to the incubation cuvette at Probe 2. The DMAE-labelled hormone occupies free binding sites on the anti-hormone antibody and the PMP-ARGG immobilizes the antibody. A set of electromagnets pulls the immobilized anti-hormone-labeled complex to the sides of the incubation cuvette and the unbound tracer is then washed out of the cuvette. Emission of light by the PMP-antibody-bound acridinium ester tracer is then induced by the addition to the cuvette of hydrogen peroxide at a low pH followed by sodium hydroxide. An inverse relationship exists between hormone concentrations in the sample and relative light units (RLU's) detected by the ACS-180.

Statistics

Statistical analyses were performed with Excel. One-tailed, paired t-tests were used to compare the men's overall hormone levels and hormone changes across the match between the two conditions (within- and between-coalition competition).

Chapter Five: Results

This chapter briefly describes the events surrounding the domino matches, presents T and C profiles for the men, and tests the hypotheses.

Within-Coalition Matches

The first day's matches were originally scheduled to take place in "Le Maine" (a pseudonym) about a two-hour walk from Bwa Mawego. Inclement weather, however, prevented our journey and instead within-coalition matches were held in the village. Participants were notified of the change and we assembled around noon at a local shop. With all subjects present, I explained that there would be two simultaneous matches and the winners would receive $15 E.C. each (about $7.50 US), and the losers would receive nothing.

Saliva was collected before the matches and I told the men to arrange themselves into teams as I set about preparing materials for the subsequent saliva collections. When I turned my attention back to the tables I was surprised to see that the dyads I had anticipated would be playing together were in the same game, but on *different* teams. Later I considered that perhaps these decisions decreased competition among these men by blurring coalitional fault lines (Patton, 2000).

The atmosphere became quite lively as several curious onlookers looked on. An almost palpable, nervous energy filled the air as play started. Fortunately, both matches followed nearly identical trajectories, which greatly simplified record keeping and timing of saliva collection. In virtual unison the laughter that had marked the early part of the matches gave way to strife, as disputes over the score erupted at both tables. Interestingly, the disputes were between the dyads I assumed were closest—the brothers at one table and the cousins at the other. The brothers resolved the dispute rather quickly but the dispute between the cousins escalated to the point that their strident pleas of rectitude actually drew the attention of the players from the other table. Their pitched disagreement lasted for the remainder of the match and lingered into the aftermath.

Both matches ended within two minutes of each other and were remarkably similar in that each team surged ahead several times. Each game ended with one team dominating the final round and emphatically slamming down the winning domino. Winners were congratulated by me and paid immediately. Matches lasted just over 25 minutes and saliva was collected according to procedures addressed in chapter four.

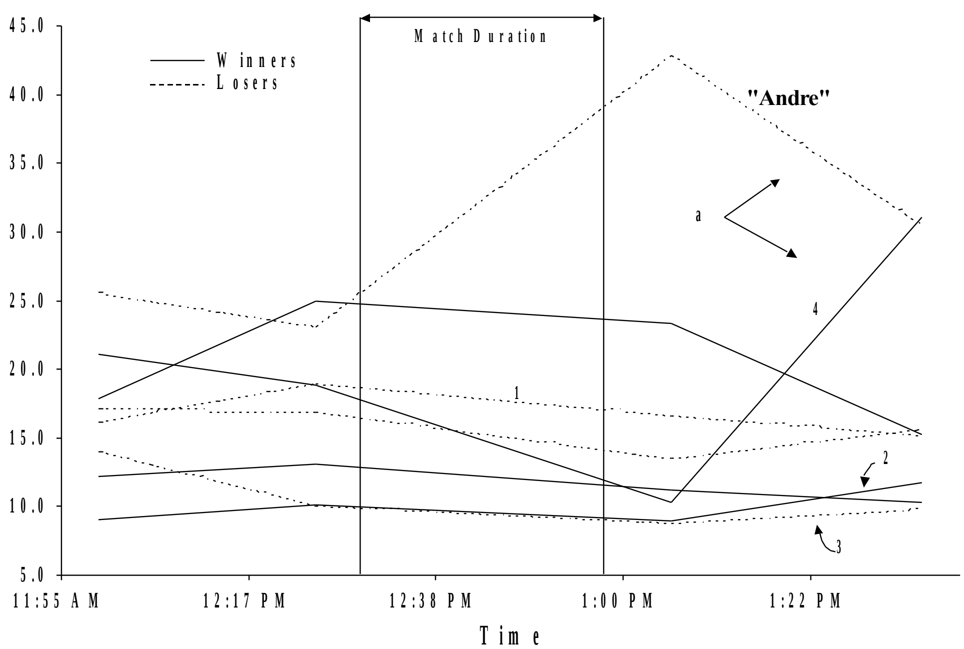

Figure 5.1 Testosterone levels for within-coalition matches. Each line represents one man. Numbers 1–4 indicate the men who would later participate in the between-coalition matches. (a) Note the different responses in these men who were in the same match but on opposite teams. Participant 4, orP4, is low status and experiences a dramatic decline in T across the

match before showing marked elevation by 45 minutes post match, while Andre, who is clearly dominant, experiences the opposite pattern (discussed below).

Four of the men experienced anticipatory rises in T and all the men, with one exception, experienced decreases in T across the match. Andre (a pseudonym) was the oldest man (36) in the matches and is by far the most physically imposing person in the entire village if not the island. He received high respect ratings (top 10%). Possibly he was least sensitive to any dominance related aspects of the competition, particularly among these men who were all clearly subordinate to him. When we consider his social predicament at the time, a scenario presents itself. Andre had recently begun consorting with a female and was preoccupied with missing a telephone call from her (she lived in a neighboring village) as he was hoping to rendezvous with her that afternoon. Thus, it may be that an anticipated sexual encounter contributed to his T elevation (Dabbs & Mohammed, 1992). Of course, a number of interpretations are possible. For instance, it could be the case that, as the clearly dominant male, his T level would have increased regardless of the outcome. Further complicating the picture, he had been suffering from insomnia for some time before the match. While a number of factors could have contributed to his dramatic response, it was rather apparent this day that his amorous preoccupation consumed him. It would ultimately prevent him from participating in the subsequent matches, much to my disappointment.

P4's dramatic rise in T following the match is worth considering. He was rated very low in status (30%), putting him in the bottom quartile. And, as I was informed shortly after the match, he had never won anything playing dominoes before (men frequently wager money or beer on matches). P4 also seems to be at somewhat of a critical juncture in his life as he enters adulthood. He is nineteen years old, was raised in an inconsistent and sometimes abusive household and has a history of erratic, and at times, violent behavior (Mark Flinn, personal communication). Additionally, he has an older brother in the village who is schizophrenic (he was last in status ratings at 18%) and often spends his days castigating villagers with crude, although occasionally insightful and hilarious, barbs. This may further compromise and complicate P4's social standing. Thus, one interpretation of P4's T response is that, as a low status and insecure male, lower T levels (he declined the most across the match) served to prevent conflict with the high status male at his table. Once the dust had settled, so to speak, his T increased.

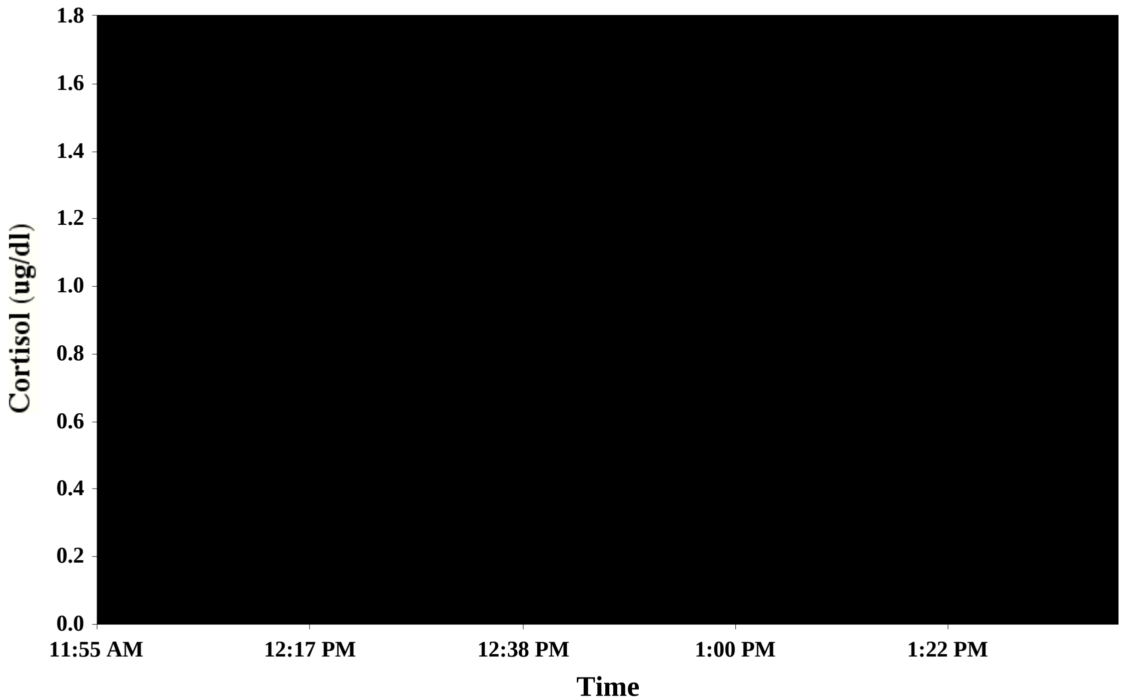

Figure 5.2 Cortisol levels for within-coalition matches. (a) Note Franklin's dramatic elevation in C before the match (discussed in text). (b) An argument occurred between these men; note that their C levels are identical before the start of the match but P2, who is the less dominant in this dyad, elevates C more than P1.

Franklin expressed anxiety and displeasure about the arrangement of the matches, which may account for his dramatic increase in C before the match. The day before he told me he didn't like that money would be given to the winners. He urged me to just buy beers for the men regardless of whether they won or lost. I explained that it was important for the men to feel strongly about whether they won or lost. He disagreed.

Between-Coalition Matches

Two days later, only four of the men (P1–4) (see Chapter Four, Study Design) accompanied me to the village of Le Maine. The men were compensated $20 E.C. each for the day's effort. We departed at 9:00 a.m. Le Maine is a two-hour walk south of Bwa Mawego. The path along the coast retraces a highway that was destroyed by hurricanes in the 1950s (see Chapter Four, Geography and General Information). There are some indications that the path was once a road, for example various stretches are broad and flat with stone structures evident, but for the most part all evidence of a former road is completely washed out. The path narrows to several inches in some places. The journey did not seem to impose much of a physical challenge for the men, although the same cannot be said for their companion.

The path opens to an agricultural area along the coast. One then takes the road across a large river, which winds up the mountainside to Le Maine. We stopped at the river to swim and collect saliva before heading up the road to Le Maine. It took awhile to arrange for the matches because most of the men from the village were out harvesting bananas. Eventually several young men were found and it was decided that the matches would be held at the bus stop, which afforded shelter from the imminent rain. The first match began at 12:20 p.m. with P1 and P2 playing two men aged 16 and 17. The second match followed immediately after the first (about one-half hour later) with P3 and 4 competing against two different men, aged 18 and 19. Matches were held in succession because not enough equipment could be located (see Chapter Four, Study Design). Additionally, there was only enough space in the bus stop to fit one table.

The first match was competitive as both teams exchanged winning hands. The score stood at 95 to 91 in our favor when a player from their team misplayed a domino—a 20-point penalty. This seemed to rattle their confidence and proved to be a blow from which they would not recover, eventually succumbing 200+ to 116 (counting stops at 200). The winners were triumphant and I congratulated them and paid them in front of about a dozen onlookers.

In the second match, participant 4 became embroiled in a vehement argument with one of the Le Maine men. After the initial salvo, this subject became extremely focused and sat at rapt attention. At one point, when the Le Maine man attempted to "kill" a hand, P4 corrected him and proceeded to slam down the next succession of dominoes to dramatic effect. A hand is considered killed when the final piece of a suit is played such that both ends of the board are the same and there are no more possible plays. The team holding the fewer points wins. Our players went on to score a convincing 200+ to 107 victory. The Bwa Mawego team was elated after the matches. The post-game victory march stopped off at a Le Maine shop and the comely young woman who served us was the subject of repeated flirtations from the Bwa Mawego team.

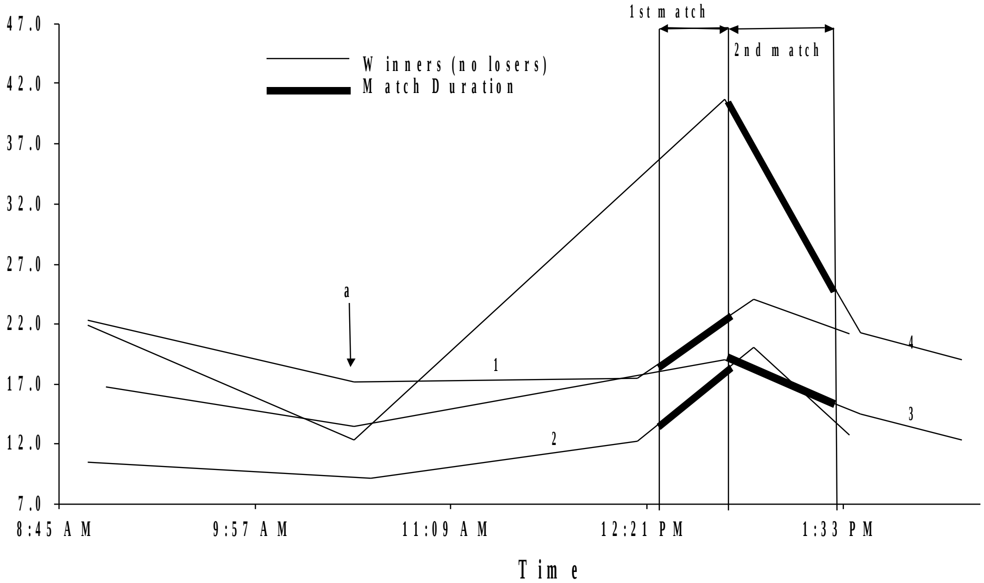

Figure 5.3 Testosterone levels for between-coalition matches. (a) All men experienced a dip in testosterone during the morning trip.

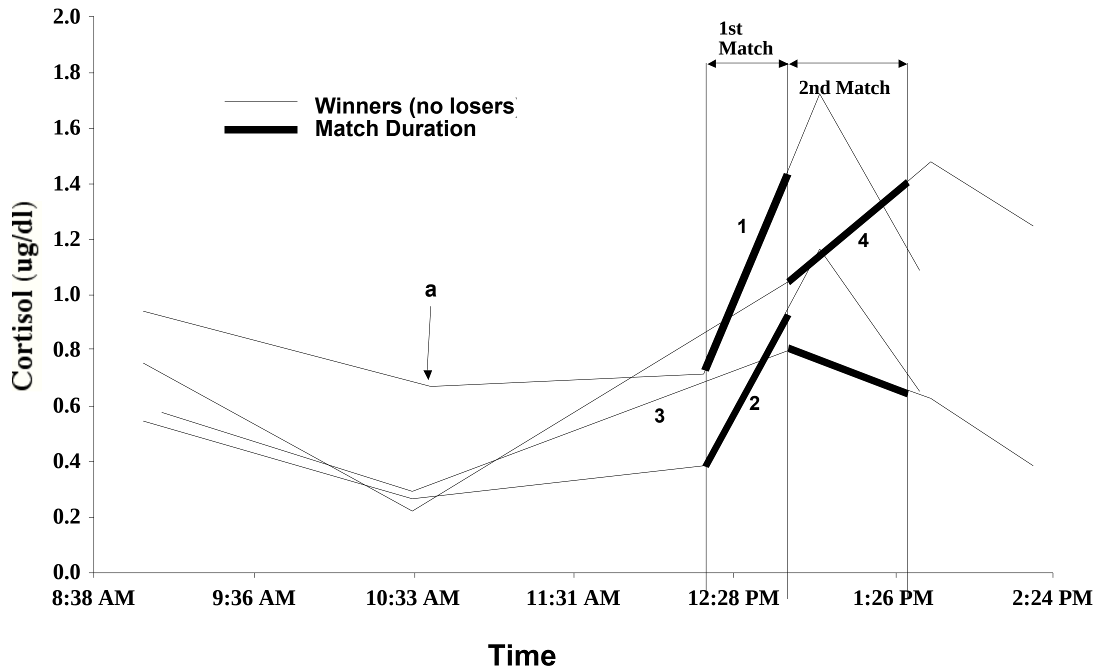

Figure 5.4 Cortisol levels for between-coalition matches. (a) All men experienced a dip in cortisol during the morning trip.

Both T and C levels decreased across the morning trip for all men, likely the result of normal circadian rhythms (Dabbs, 1990b). Note that P4 continues to show marked increases in C despite having experienced vicarious arousal (discussed below); this likely stemmed from his argument during the match.

Tests of Hypotheses

The main objective is to determine whether coalitional context affects hormone response to competition. Overall hormone levels and changes in hormone levels across the matches are compared for the within and between coalition competition conditions.

Hormone Levels

T and C levels from before and after the matches (three values) were pooled to generate an overall hormone response measure for each individual. This was necessary because the within-coalition matches were held simultaneously, whereas between-coalition matches had to be held consecutively because of a lack of materials. Thus, Ps 3 and 4 witnessed the first between-coalition match and appear to have experienced vicarious hormone elevations from watching (e.g. Bernhardt et al., 1998; Kemper, 1990), and hormone levels tend to show rebound effects after elevating (Kanaley et al., 2001). As a result, repeated-measures ANOVA test was not applicable because the hormone measurement times were not necessarily identical.

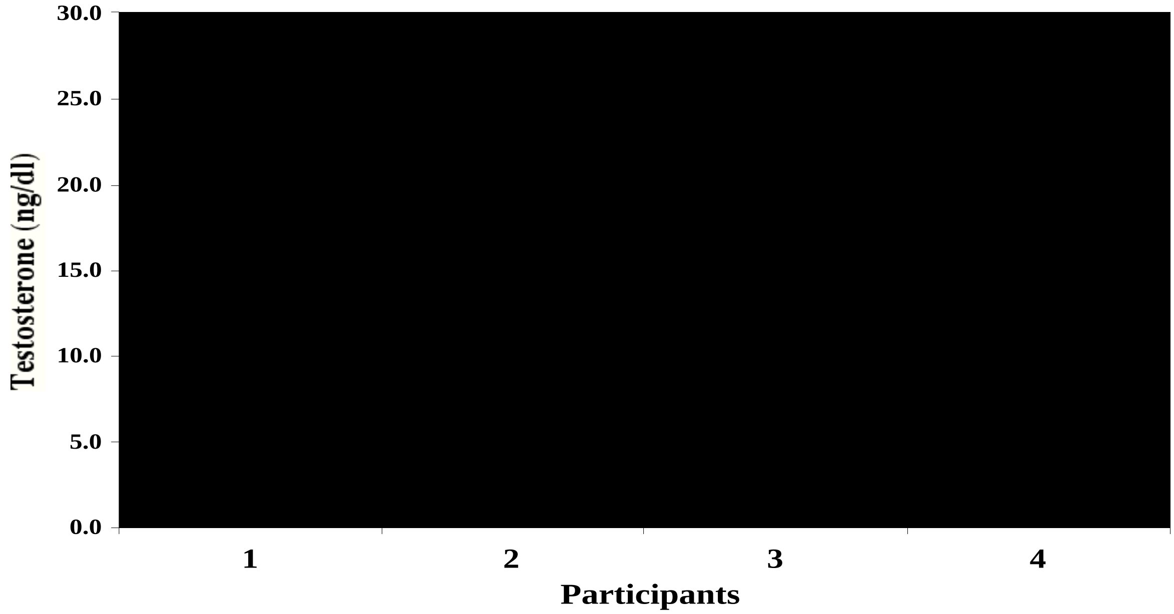

Figure 5.5 Average testosterone levels during within- and between-coalition matches for each participant.

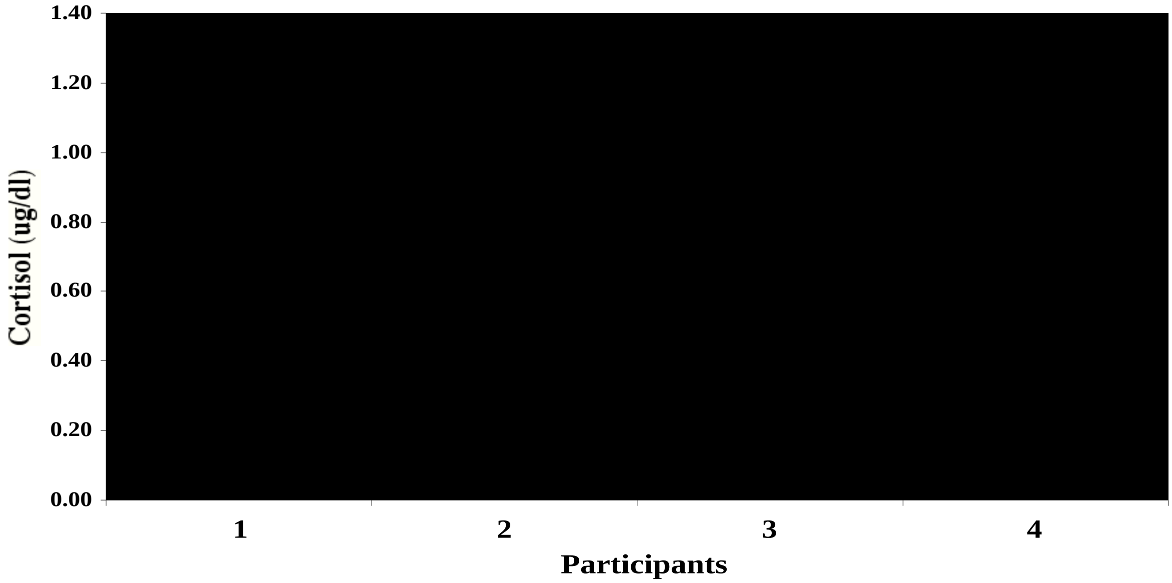

Figure 5.6 Average cortisol levels during within- and between-coalition matches for each participant.

One-tailed, paired t-tests indicated that both T ($p = .024$) and C ($p = .024$) levels were significantly ($p < .05$) higher during between-coalition competition than during within-coalition competition. Further, this effect was consistent in all men. Recall that T levels tend to increase in winners relative to losers. In figure 5.5, all of the men won the between-coalition matches, but P1 and 3 lost their within-coalition matches, which may have contributed to their lower T level. However, after showing decreases in T across the within-coalition matches, P3 actually increased his T level slightly between 15 and 45 minutes after his loss although P1 continued to decline slightly. Therefore, it is possible that losing the within-coalition match contributed to between-coalition T level being higher for P1 but not for P3.

Hormone Change Across Matches

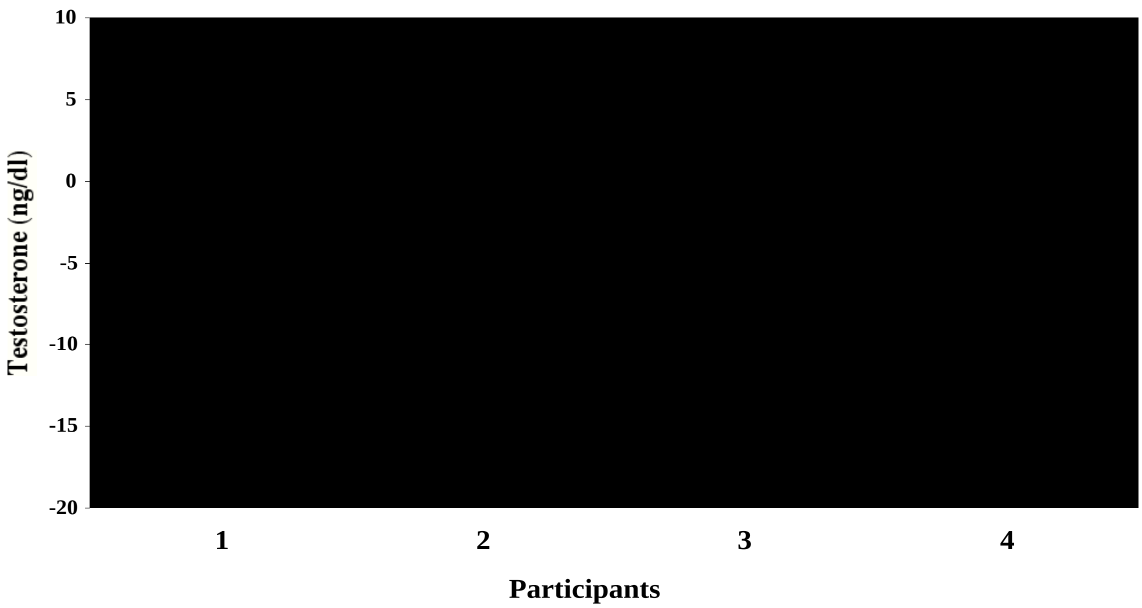

Figure 5.7 Change in testosterone levels for each participant from immediately before to 15 minutes following the conclusion of within and between coalition matches.

Figure 5.8   Change in cortisol levels for each participant from immediately before to 15 minutes following the conclusion of within and between coalition matches.

One-tailed, paired t-tests indicated that absolute changes in T were significantly different ($p = .018$) for within- and between coalition competition, but not for C ($p = .062$). These values should be considered in light of the small degrees of freedom. Bars represent hormone changes across matches, which were greater for all men in the between-coalition matches. Recall that P3 and P4 likely experienced vicarious hormone elevation before the start of their matches and this probably accounts for the decrease in their T levels across the between-coalition match. Although note that P4 continued to increase his C level, likely in response to the argument. The argument between P1 and P2 during their within-coalition match (they were on separate teams) is reflected in their C levels in figure 5.8. Note however that their C elevation across the between-coalition match was still *higher,* indicating that between-coalition competition is a potent trigger for C release.

Ratio of T to C (T/C)

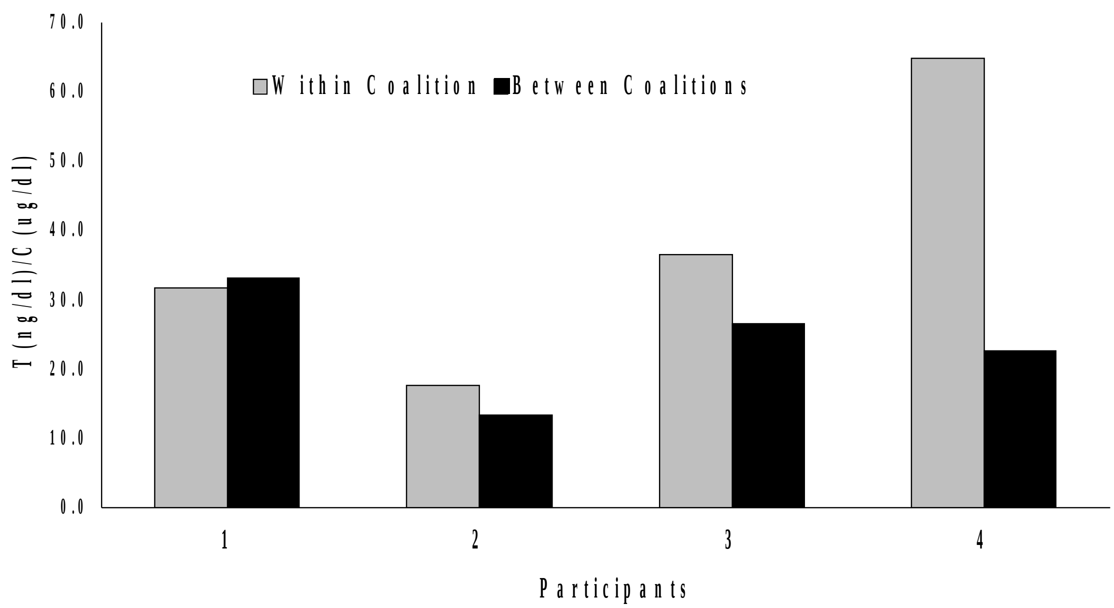

Figure 5.9 Ratio of T to C. Bars represent average T values over average C levels for each participant.

All participants except for P1 show lower T/C ratios during between-group competitions than in the within-group matches, indicating that C was elevated higher than T. Within-coalition T/C ratios would have been higher for P1 and P2 were it not for the C increase associated with their argument.

Chapter Six: Discussion and Conclusions

Results indicate that hormone response to competition between coalitions is more marked than competition within a coalition in this sample of men. Both T and C levels were higher and hormone changes across the matches were more pronounced. Also, C elevated more than T in response to the between-coalition matches. These findings suggest that male coalitions are an important contextual factor modulating endocrine responses to competition

This study builds on a growing body on research on human hormone response to competition (Booth, Mazur, & Dabbs, 1993; Booth et al., 1989; Dabbs & Dabbs, 2000; Elias, 1981; Gladue, Boechler, & McCaul, 1989; Gonzalez-Bono et al., 1999; Mazur & Lamb, 1980; Mazur, Susman, & Edelbrock, 1997; Mazur, Booth, & Dabbs, 1992; McCaul, Gladue, & Joppa, 1992; Salvador et al., 1987; Serrano et al., 2000) and adds to previous research efforts into contextual factors affecting human hormone function (Flinn & England, 1997; Flinn, 1999; Kirschbaum et al., 1995; McDade & Worthman, 1998; Thorsteinsson et al., 1998). By combining these two areas, this study provides a unique contribution to the literature.

The broader theoretical implications of these findings are that human males appear to react differentially, through hormonal mechanisms, to within- and between-group competition. This may be taken as evidence in support of Alexander's social competition hypothesis (1989) in that selection has shaped human hormone systems (and cognitive mechanisms) to differentially respond to these two types of competition. Of course, further research is needed to more fully address this issue.

There were some indications for a number of phenomena that suggest interesting possibilities. For example, T increases following victory appear to have been delayed somewhat for the within-coalition matches, although this wasn't specifically tested. Status rankings may be important. For example, a low-status male may delay T increase after victory if it comes at the expense of a higher-ranking male. One interpretation is that tightly knit social units have more complex repercussions that are being sorted out during the aftermath of an encounter. The manner in which the men arranged teams for within-coalition matches may have also served to militate against overt dominance competition between dyads by preventing the closest allies from cooperating together.

If T elevations signal dominance (Mazur & Booth, 1998), there are likely to be costs associated with these responses, otherwise we would expect all men to continually elevate their T levels. Costs include not only metabolic—it is energetically expensive to manufacture anabolic T—but perhaps also behavioral costs. Increasing T is probably only adaptive in specific circumstances such as those involving a status elevation, a sexual encounter perhaps, or during extreme (intergroup?) competition. This calls into question elevating T through artificial means. While restoring T to normal or functional levels seems to be therapeutic for hypogonadal men (Booth, Johnson, & Granger, 1999a), raising T above this range will likely result in significant trade-offs.

In chapter two an analogy was drawn between human male coalitions and baboons resembling each other in terms of status and hormone profiles. As Sapolsky has demonstrated, high-status males, or males engaging in fitness enhancing behaviors such as copulations and ability to discern meaningful threats (Ray & Sapolsky, 1992), have lower hormone levels when their groups are stable and are able to elevate hormone levels more in response to stress than are subordinates (1990—1992). Therefore, it is possible that this might also be the case for humans. If so, one intriguing possibility is that the overall lower T levels found in non-western men could be partially attributed to living in stable coalitions, in addition to energetic constraints (Bribiescas, 1997; Ellison et al., 1998).

Strengths

One of the strengths of this study is that domino was an effective method for stimulating dominance competition in this population. The overall level of interest and excitement shown by the participants, and their concern over the outcome—recall the vehement arguments—support this contention. Additionally, changes in hormone levels during the competitions were reliable, also consistent with the idea that the men were engaged in the matches.

Bwa Mawego is an ideal place to study male coalitions. Villagers are life-long acquaintances and men have developed strong social bonds from long-term interactions. Also, this population lives in more naturalistic social conditions—surrounded by kith and kin—than can be found in any industrialized nation, which is useful when attempting to test hypotheses concerning ancestral conditions, or the environment of evolutionary adaptation (EEA) (Tooby & Cosmides, 1992).

Limits

The major limit of this study is the sample size, which prevents drawing strong conclusions. However, the magnitude of the findings suggests that the effect is meaningful and warrants further investigation.

To some degree, the men who were selected to participate were assumed to constitute a natural, or pre-existing coalition. Working on a short time scale, it was not possible to delve intimately into the social lives of the men, and other methods were necessary for obtaining a suitable sample (see Chapter Four, Participant Selection). It is possible that extenuating circumstances could have compromised the integrity of the coalition unbeknownst to me, such as an ongoing rift between two men. This might skew the results towards higher hormone levels, or more arousal, for within-coalition competition, particularly if the men were on opposite teams. However, one of the premises of this study is that mechanisms for defusing competition operate within coalitions and are reflected by lower hormone responses. A more naturalistic experiment might involve having men self-segregate themselves into coalitions, or ideally, finding smaller coalitions of men that are split along kin lines, such as occur in Yanomamo villages, and are relatively immune to coalition building within groups. One would expect differences in hormone response to within- and between-group competition to be even more profound in these circumstances.

Basal hormone levels were not determined in these men. As Sapolsky has shown in baboons (1991; 1992), knowledge of basal hormone levels can contribute to interpreting hormone responses to stress. In connection with this, personality was also not assessed, which could have contributed information about individual differences in hormone responses.

Caution is also advised in interpreting single hormone measures because of circadian cycles and pulsatile release of hormones (Norman & Litwack, 1997), which can indicate artificially high hormone levels. This is not of especial concern in this study because hormone levels were assessed temporally. Except for P4, who consistently showed wide variability in hormone levels, none of the other men appeared to have outlying measurements.

Also, information concerning the men's morning activities was not systematically collected. Sexual encounters and physical exercise, for example, have been shown to affect T levels (Dabbs & Mohammed, 1992; Kuoppasalmi et al., 1976). It is possible that these activities could have affected pre-match T levels and subsequent responses, although I did informally inquire about exercise before the within-coalition matches and about sexual activity the morning before the between-coalition matches (I assumed nobody had exercised before 9:00 a.m.).

Another concern is that the winners received money. It may be the case that losing money to a good friend is not very upsetting because one anticipates that the winnings will be shared, which could have contributed to lowered hormone response to the within-coalition matches. However, strong reactions to winning and losing militate against this possibility. Alternatively, one man, Franklin, appeared to experience acute anxiety before the within-coalition match precisely because there *was* money involved. This highlights the importance of considering social-contextual variables that may not be the primary focus of a study.

Individual differences in the significance attached to the matches and outcomes may have affected the results. For example, dominant males may have little reaction to winning or losing against a subordinate, as may have occurred with Andre. Subordinates, meanwhile, may have attached more significance to victories over high-ranked males. These possibilities are not fatal for this study, but should be incorporated in future studies.

Future Directions

Replicating these findings in a larger sample of men is warranted. Other variables to consider include individual variability in baseline hormone levels and the interaction of personality factors with hormone response. For example, Eubank et al. (1997) found consistently lower C levels, more rapid catecholamine elevation, and higher T response as time to event approached in elite canoeists perceiving their pre-competition anxiety positively rather than negative. Other personality factors are worth examining and efforts in this direction have been reported (Schultheiss et al., 1999).

Currently, most studies of hormone response to competition have used male subjects. Aside from a possible bias to do research on males, it is true that T is roughly ten times higher in males than females and it is therefore easier to detect T fluctuations at the low levels found in saliva. Also, male competition is much more overt than female competition (Geary, 1998), and T responses to competition are more easily interpretable in terms of dominance (Mazur, 1985; cf. Cashdan, 1995). This study focused on male coalitions because, in humans, males predominantly engage in coalitionary aggression (Chagnon, 1992; Wrangham & Peterson, 1997), and one of the intended purposes was to determine if this behavior resulted in selection on human (neuro)endocrine systems. However, in most primate species, females predominantly engage in intergroup aggression (Cheney, 1987) and for humans, female coalitions are still an important means of competition for resources even if this competition is conducted more through social relationships (i.e., gossip) than overt aggression (Geary, 1998). Interesting sex differences are surfacing in how males and females react hormonally to social situations (Mazur, Susman, & Edelbrock, 1997; Taylor et al., 2000). Studies of female coalitions, and hormone response to competition are in their infancy, and as such, should provide ample opportunities for research.

Other contextual factors could prove illuminating, such as whether competition occurs on familiar territory or not, which may differentially engage mechanisms for spatial orientation and memory. Different forms of competition, particularly culturally specific forms, are needed to verify this phenomenon with particular attention paid to the mores of the society. That is, might there be an egalitarian ethos that is contributing to high levels of cooperation and hence, lower hormone response to within-group competition? Cultural considerations could possibly be contributing to the repeated failure to find significant outcome-dependent changes in hormone levels in Spanish judoists (Salvador et al., 1987; Suay et al., 1999). Additionally, competition for more immediate resources, such as mates, may result in more serious competition and as such, stimulate different hormone responses.

Examining different coalition sizes might provide insight into ancestrally relevant patterns of coalitional competition. Caporael's (1997) core configurations model suggests that repeated assemblies of face-to-face group settings (dyad, 5, 30, 300) were the selecting environments for human cognition. Similarly, particular sized coalitions organized for competition may elicit different (hormone) responses from individuals. As Mischel and Shoda (1995) point out, an individual who is socially dominant in a dyad may not act socially dominant in a larger context (e.g., five people working a problem). It is therefore highly probable that an individual's hormone response to competitive situations will directly depend on who is involved, as well as other tangential relationships of the participants.

A fundamental concern for any of these studies will be to understand how T and other hormones actually influence cognition and behavior, and interpreting the evolutionary significance of how these mechanisms operate. Hormone structures are highly conservative across phyla indicating that hormones have acquired various, albeit related, functional roles in different species. Therefore, investigation of endocrine mechanisms, such as for the regulation of social behavior, will require increased understanding of the localized effects of T in the brain including receptor distribution (Insel & Young, 2000), as well as interactions with hormones such as C, and how all of these operate in recursive social contexts. The addition of other hormones into the investigative mix is welcomed. In the realm of male coalition building, oxytocin, prolactin, and possibly vasopressin, are likely candidates for involvement in the formation of male bonds along with T and C (Geary & Flinn, in press).

Conclusions

It is unlikely that human hormone response to competition is as simplified as current models assume. Important factors to consider include individual variability in hormone systems and development, personality characteristics including status, social context, and sex differences (Geary & Flinn, in press). This study investigated male coalitionary context as a potential factor influencing hormone response to competition and findings were consistent with this interpretation. The ability to form, compete as, and live in coalitions was a key development in our evolution and is probably unique in the degree that it is found in humans (Alexander, 1987; Geary & Flinn, 2001; cf. de Waal & Harcourt, 1992). As such, examining the implications arising from this behavioral pattern holds great potential for understanding our species, including the functions of hormone responses to social situations. Hormone mechanisms may mirror the complexity of the social environment in which they were designed to operate.

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