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Prestige in a Large-Scale Social Group Predicts Longitudinal Changes in Testosterone

Joey T. Cheng
University of Illinois at Urbana-Champaign

Olga Kornienko
George Mason University and University of California, Irvine

Douglas A. Granger
University of California, Irvine and Johns Hopkins University

In many social species, organisms adaptively fine-tune their competitive behavior in response to previous experiences of social status: Individuals who have prevailed in the past preferentially compete in the future, whereas those who have suffered defeat tend to defer and submit. A growing body of evidence suggests that testosterone functions as a "competition hormone" that coordinates this behavioral plasticity through its characteristic rise and fall following victory and defeat. Although well demonstrated in competitions underpinned by *dominance* (fear-based status derived from force and intimidation), this pattern has not been examined in status contests that depend solely on *prestige*—respect-based status derived from success, skills, and knowledge in locally valued domains, devoid of fear or antagonism. Thus, the hormonal mechanisms underlying prestige-based status are largely unknown. Here, we examine the effects of previous experiences of prestige—assessed using community-wide nominations of talent and advice provision—on intraindividual changes in testosterone in a large-scale naturalistic community. Results revealed that men who achieve high standing in the group's prestige hierarchy in the initial weeks of group formation show a rise in testosterone over the subsequent 2 months, whereas men with low-prestige show a decline or little change in testosterone—a pattern consistent with the functional significance of context-specific testosterone responses. No significant associations were found in women. These results suggest that the long-term up- and downregulation of testosterone provides a mechanism through which past experiences of prestige calibrate psychological systems in a manner that adaptively guides future efforts in seeking and maintaining prestige.

Keywords: hormones, prestige, social hierarchy, social status, testosterone

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In a wide range of species, including humans, prior social interactions with conspecifics modulate subsequent behavior, influencing standing in dominance hierarchies, territorial formation, access to mates, and even the outcome of future agonistic conflicts with unacquainted opponents (Pusey & Packer, 1977). Despite the prevalence of these effects on ecologically relevant social structures across the animal kingdom, however, their evolutionary and proximal significance remain not well understood (Rutte, Taborsky, & Brinkhof, 2006). One prominent approach to this issue proposes that an organism's testosterone (T), a principal androgen regulated by the hypothalamic-pituitary-gonadal (HPG) axis—responds flexibly to current social environmental conditions in an adaptive and predictable manner capable of coordinating an integrative behavioral response (Hirschenhauser & Oliveira, 2006;

Joey T. Cheng, Department of Psychology, University of Illinois at Urbana-Champaign; Olga Kornienko, Department of Psychology, George Mason University, and Institute for Interdisciplinary Salivary Bioscience Research, University of California, Irvine; Douglas A. Granger, Department of Psychology and Social Behavior, University of California, Irvine, and School of Nursing, Bloomberg School of Public Health, and School of Medicine, Johns Hopkins University.

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Correspondence concerning this article should be addressed to Joey T. Cheng, Department of Psychology, University of Illinois at Urbana-Champaign, 603 East Daniel, Champaign, IL 61820. E-mail: jtcheng@illinois.edu

Wingfield, Hegner, Dufty, & Ball, 1990). This approach predicts that social interactions, especially those involving intraspecific competition, act to modulate changes in T levels, which in turn mediate androgen-dependent behaviors, motivations, and cognitions (e.g., persistence, competitiveness, status displays, risk-taking, aggression). By activating this suite of cognitive and behavioral adaptations, T serves as a competition hormone that readies individuals for the pursuit and maintenance of status, thus effectively maximize individual net fitness in competitive interactions. In the research reported here, we extend this work on the social modulation of T in humans by investigating whether and how an individual's existing prestige standing—a form of social status based upon skill, success, and respect—in a large-scale social community relates to subsequent prolonged changes in his or her T levels over a 2-month period.

Social Status and Testosterone

The aforementioned theoretical framework, and the predictions it generates regarding the links between status competitions and T, organizes a large, interconnected array of empirical findings in diverse species, including humans (Eisenegger, Haushofer, & Fehr, 2011). These findings can be parsed into two closely related lines of research, which we summarize below. The first addresses the long-pondered question of whether and how T confers social rank, and the second line considers the ways in which T responds dynamically to victory and defeat in rank contests.

Does Testosterone Drive Status-Enhancing Behaviors and Influence Rank?

One central line of inquiry in the T and behavior enterprise focuses on the cognitive and behavioral effects of T to understand how this competition hormone readies and fires up individuals' status-seeking motivations, behaviors, and strategies to produce a complex, integrated behavioral repertoire well-designed to increase one's relative status. These studies reveal that T is associated with a heightened motivation for status, as well as the increased frequency and intensity of behaviors and psychological states that increase the likelihood of achieving and maintaining, status. Of these, three particularly compelling sets of findings come from (a) Josephs, Sellers, Newman, and Mehta (2006), who show how the assignment of individuals with high T to a low-status treatment induces substantial distress by eliciting negative affect and physiological arousal, bolstering attentiveness to status cues, and suppressing cognitive functioning and performance; (b) Mehta, Jones, and Josephs (2008), who show how cortisol—a neuroendocrine marker of stress—rises among high T individuals who lose status by suffering a defeat in a competition, but drops among high T individuals who gain status by winning; and (c) Mehta, Lawless DesJardins, van Vugt, and Josephs (2017) and Slatcher, Mehta, and Josephs (2011), who found that men with high circulating T showed more characteristic dominant ethological displays, including self-entitling and assertive gestures and verbal statements, and disproportionate claims to shared resources. Complementing these findings, laboratory studies, some of which involve exogenous administration of T to establish causality, also reveal the effects of circulating or rising T on propelling traits that heighten competitiveness, including persistence (Andrew & Rogers, 1972; Archer, 1977), competitive motivation (Carré & McCormick, 2008; Coates, Gurnell, & Rustichini, 2009; Mehta & Josephs, 2006), and reduced stress and fear (Hermans et al., 2007; Hermans, Putman, Baas, Koppeschaar, & van Honk, 2006), or capabilities that contribute to the likelihood of future success, such as memory and learning (Ackermann et al., 2012; Wright, Edwards, Fleming, & Dolan, 2012), and cognitive acumen (Coates et al., 2009; Janowsky, Oviatt, & Orwoll, 1994; Newman, Sellers, & Josephs, 2005; O'Connor, Archer, Hair, & Wu, 2001; Zilioli & Watson, 2014). These lines of evidence suggest that T is crucial for understanding the determinants of when and why individuals strive to out-excel others in rank and high status behaviors (Mazur & Booth, 1998).

These empirically supported effects of T on status motivation and ethologies, however, must be distinguished from the question of T's *actual effectiveness* in promoting social status. Of course, all else being equal, individuals with elevated T who expend most effort in competing for status and improving their social standing should—by virtue of their greater competitiveness, ambition, persistence, and efforts in status signaling—also enjoy greater success at inspiring deference and achieving influence in the community, compared to their less invested counterparts. However, a crucial (yet frequently overlooked) consideration in whether status is effectively achieved by status-seekers is that emergent status asymmetries, like most behavioral outcomes, is the result of highly complex interactions among a large number of variables. These include the status-relevant traits, assets, and behaviors of the status-seeker, the traits, assets, and behaviors of other prospective status competitors, the mutual relative competitive ability of the status-seeker vis-à-vis the opponent(s), as well as the local norms of the social group (or institution; R. F. Oliveira et al., 2016). For these reasons, a highly motivated status-seeker's attempts to assert and signal her status may fail to generate substantial gains in status and deference because of a host of factors, such as her below-average performance, her exceptionally talented peers, the existence of unique norms in the local group that actively suppress status signals and asymmetries, or a combination of all of these and other factors.

This line of reasoning suggests that, although T propels a specialized battery of cognitive states (including the suite of biases that can be collectively described as status motivation) and behaviors jointly designed to enhance one's relative status standing, the link between T and actual emergent rank is expected to be highly variable (i.e., emerging in some contexts but not others) and modest at best in most environments (i.e., T may be weakly correlated with actual status, despite a relatively stronger link with status motivation). The application of this logic has led numerous researchers to conclude that a simple one-to-one association between T and actual rank—or more broadly, the notion of a single "hormonal profile of rank"—is unlikely to be tenable. For example, a key insight that Robert Sapolsky gleaned from his seminal work on primates is that "there is no single testicular profile of dominance", because "the physiological correlates of rank [(such as T)] do not cause rank; in most studies of captive primates, [T] concentrations prior to group formation do not predict eventual rank" (Sapolsky, 1991, p. 290) Similarly, after reviewing the relevant empirical evidence cumulated across five decades, anthropologist and primatologist Patricia Whitten proposed that:

> endocrine studies in male primates were undertaken originally in order to identify the physiological attributes that confer dominance. This goal proved elusive, in part because it suffered from several misperceptions. . . . Although there may be some intrinsic qualities of the individual that increase success in competitive encounters. . . . A consistent endocrine profile of dominance would not be expected because hormones are responsive to social interactions and because dominance is a social relationship rather than a property of the individual. (Whitten, 2000; p. 276)

Supporting this broad view, much empirical evidence increasingly suggests a mixed link between T and rank in humans, with studies in both the laboratory and the field indicating either a weak or null association between T and the distribution of trait or emergent status (e.g., Akinola, Page-Gould, Mehta, & Lu, 2016; Dabbs, Hopper, & Jurkovic, 1990; Johnson, Burk, & Kirkpatrick, 2007; Josephs et al., 2006; Sherman, Lerner, Josephs, Renshon, & Gross, 2015; Slatcher et al., 2011; van der Meij, Buunk, van de Sande, & Salvador, 2008; van der Meij, Schaveling, & van Vugt, 2016; for an expanded discussion, see electronic supplemental material). In perhaps the most relevant study (Mazur, Welker, & Peng, 2015), rank distributions were examined within small groups of three men who took part in a leaderless, unguided 10-min conversation in the laboratory. Emergent rank and leadership—as measured by a combination of indices including speaking time and group members' nominations of who led the group—was not associated with circulating T pre- or postinteraction, even in groups in which high-rank is rewarded with monetary incentives (paralleling the evolutionary incentives to high-ranking individuals). It is important to realize, however, that this variable effect of T on rank asymmetries does not contradict T's reliable effect on status-enhancing behaviors and cognitions. The key insight from this is that, although empirically any straightforward and robust link between T and emergent rank across a range of studies is improbable, theoretically T can lead to probabilistic increases in the likelihood of acquiring high rank in certain conditions and circumstances, though the effect may be weaker than one might expect based on folk wisdom regarding the behavioral effects of testosterone (Eisenegger, Naef, Snozzi, Heinrichs, & Fehr, 2010).

Does Testosterone Respond Dynamically to Success and Defeat in Social Interactions?

A second major complementary line of work in the T and behavior enterprise considers how T release may itself be influenced by success in rank competitions.[1] That is, rather than address whether T is a causal agent of rank-seeking behavior, this line of research instead explores how T dynamically *responds* to social context. This body of work reveals that a wide range of social mammals calibrate their T levels to previous history of wins and losses in rank contests (Mazur & Booth, 1998). Winners of status contests generally show a rapid increase in circulating T relative to precompetition or losers in physically demanding competitions, such as wrestling and tennis (Booth, Shelley, Mazur, Tharp, & Kittok, 1989; Elias, 1981; Mazur & Lamb, 1980), as well as nonphysical competitions with sanctioned competitors, such as chess matches (Mazur, Booth, & Dabbs, 1992). Of note, these victory-dependent transient changes in T suggest that in humans—a group-living species who possess membership in (and frequently move freely between) numerous social groups (from small pair-bonded relations to large aggregations), each with their own within-group asymmetries—circulating T levels are likely constantly in flux to mirror our current rank in the most salient social context. Thus, this responsiveness of T to social environment provides yet another reason to expect a weak or null association between one's baseline T and social rank in any one given group.

One potential problem in these earlier studies demonstrating context effects, however, is that causality cannot be firmly established: surges in T may be a physiological mediating cause (rather than consequence) of winning, opening up the question of whether relative status causally influences T. However, recent laboratory experiments using rigged competitions to manipulate wins versus losses to control for interindividual differences in basal T confirm a causal effect of winning on elevated T (Gladue, Boechler, & McCaul, 1989; Zilioli & Watson, 2012, 2014; but see Wu, Eisenegger, Sivanathan, Crockett, & Clark, 2017), even when the outcome is entirely chance-based (e.g., coin-tosses; McCaul, Gladue, & Joppa, 1992) and victory is experiential rather than personal, such as in fans of a winning soccer team and supporters of a winning political candidate in an election (Bernhardt, Dabbs Jr, Fielden, & Lutter, 1998; Stanton, Beehner, Saini, Kuhn, & LaBar, 2009). This causal effect of winning on T can be sizable; for example, simply watching one's previous victory on video can produce a 40% T increase (Carré & Putnam, 2010). Together, this existing body of evidence suggests that, in many social mammals, victory-dependent endocrine changes—combined with other status-dependent changes in morphology (e.g., alterations in facial coloration and other sexual adornments, testicular size) and behavior (e.g., sociality) that occur when adult males rise or fall in social contests—is part of a broader suite of behavioral and physiological adaptations for regulating hierarchy formation and reproductive contests (Setchell & Dixson, 2001; Wingfield et al., 1990).

In sum, these diverse lines of evidence support the notion that T may function as a competition hormone that (a) calibrates psychological systems to current social standing and other prior interactive experience to adaptively guide status-seeking efforts, (b) acts as a physiological modulator of future intention and behavior, including signaling achievement or self-perceived status and sustaining competitiveness, and (c) more broadly motivates and guides status-seeking efforts in a manner that takes into account current conditions to most effectively exploit available opportunities for status attainment. Thus, the social effects of T may be best interpreted as reflecting a responsive system that reflects and reinforces status by readying and facilitating behavioral and cognitive responses geared toward acquiring, signaling, and sustaining social status. Under this framework, insights into the interactions between T and social status are crucial for understanding not only biological states but also key aspects of human social behavior.

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[1] A third major program of research, not reviewed here because of space constraints, explores how T governs differential investment in mating and parenting efforts (Archer, 2006; Gettler et al., 2011; Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002; Wingfield et al., 1990).

Social Status and Testosterone in Humans: Disentangling Dominance and Prestige

Though this existing literature contributes substantially to exploring the psychological and biological foundations of social status, a key shortcoming of this body of work is that it has thus far not attended to a key distinction between different forms of status in human societies. These studies have tended to assume that human status is simply an extension of primate dominance hierarchies. However, a large enterprise on understanding the evolution of culture and the coevolution of culture and genes has proposed that human's reliance on cultural learning has led to the emergence of a separate form of status, termed *prestige*, that explains why people preferentially defer to and are persuaded by individuals who are particularly successful, skilled, and knowledgeable in locally valued domains (Boyd & Richerson, 1985; Boyd, Richerson, & Henrich, 2011; Henrich & Gil-White, 2001). This theoretical work proposes that, upon the evolution of cultural learning capacities in our lineage, natural selection favored the propensity for individuals to bias their attention, imitation, and advice-seeking efforts toward successful individuals in order to gain proximity and opportunity to learn and acquire high quality information from these prestigious models. Prestige contrasts sharply with *dominance* status seen in other social mammals, which is primarily based on coercive capacity derived from strength, force, threat, and intimidation.[2]

Confirming this distinction, a substantial body of laboratory and field evidence has emerged to reveal that prestige and dominance can (a) be distinguished by their ethological displays (e.g., postural and vocal cues and signals (Cheng, Tracy, & Henrich, 2010; Cheng, Tracy, Ho, & Henrich, 2016), motivational profiles (Case & Maner, 2014; Maner & Mead, 2010; Mead & Maner, 2012), and affective responses (Cheng et al., 2010) and (b) coexist to influence group decision-making and attention patterns (Cheng, Tracy, Foulsham, Kingstone, & Henrich, 2013), high status displays (Shariff & Tracy, 2009; Tracy & Robins, 2004), and mating and reproductive success (Snyder, Kirkpatrick, & Barrett, 2008; von Rueden, Gurven, & Kaplan, 2011).

Having yet to recognize this distinction, however, existing empirical studies exploring the connection between social status and T tends to treat status as a uni-dimensional construct and frequently operationalizes it as a mix of both prestige and dominance. In these studies, T is examined primarily in physically taxing sports competitions (e.g., wrestling, tennis) that emphasize both physical prowess (e.g., size and strength, agility, endurance)—which may induce submission via perceived force and coercion (dominance)—and other game-relevant skills and abilities (e.g., planning, strategizing, technique) that may attract deference based on earned respect for perceived success and achievement, giving rise to prestige. This context of study, coupled with the use of competition outcomes (winning vs. losing) as a window into relative status without measuring subjective assessments of status, means that these studies unknowingly capture a confusing mix of dominance and prestige psychological processes and their effects on T. Though some other work has examined skill-based contests that lack physical confrontation (e.g., chess, tetris), these studies are also potentially plagued by this issue because any direct competition with a sanctioned rival or enemy is likely to evoke a dominance psychology based on domination and subordination generated by interindividual or group animosity and hostility, in addition to prestige stemming from greater intellectual skill. As a result, the existing work, bedeviled by this lack of theoretical clarity, leaves open the question of whether the T effects obtained are spurred solely by prestige or dominance status processes, or both simultaneously.

In the present research, we strive for clarity and seek to test whether T responds to changes in prestige-based social standing devoid of dominance. We focus on how T responds to success in prestige contests, rather than the effects of T on prestige-based rank, because of the complexities enumerated above regarding T's anticipated weaker and more variable effect on actual rank asymmetries (which also applies to prestige hierarchies). By contrast, the rise and fall of T in response to competitive outcomes is well documented (Geniole, Bird, Ruddick, & Carré, 2017), thus providing a suitable point of entry into understanding how T and rank acquired solely via earned merit and achievement—which has received little empirical attention compared to strictly dominance-based rank—may interact. Our focus here on T responses to prestige-derived rank therefore contributes to growing theoretical efforts to explain (a) how endocrine signals act as physiological intermediaries between variable environmental input conditions and fine-tuned, adaptive responses to these conditions (R. F. Oliveira, 2004; Roney, 2016) and (b) how prestige and prestige competitions operate to influence human psychology, ethology, and sociology (Cheng et al., 2013, 2010, 2016; Henrich, Chudek, & Boyd, 2015; Henrich & Gil-White, 2001; Maner & Case, 2016; von Rueden et al., 2011).

To unambiguously distinguish prestige from dominance, we focus on how T changes in accordance with experiences in attracting respect and admiration from one's coalitional in-group. Notably, our focus on a collegiate marching band—a social group that is principally organized and motivated by a cooperative collective goal, and for which prestige depends primarily on musical performance and coordination in marching (rather than muscularity and aptitude for physical conflict as in athletic groups)—provides a particularly suitable model social context for empirically isolating prestige from the dominance dimension of status. In further effort to empirically disentangle these two forms of rank, we assess and use the distribution of perceived force and coerciveness as a control in order to examine the effects of prestige on T, unconfounded by dominance. Consistent with the theoretical distinction between these varieties of status (Cheng et al., 2013; Henrich & Gil-White, 2001), our assessment of prestige focuses on

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[2] Note that the concept of dominance has different definitions across, and even within, disciplines, which can generate considerable confusion (for an overview, see Cheng et al., 2013, Table 1). Here, we mean a form of status based on fear and coercion that results from relatively greater strength, intimidation, and imposition (i.e., the ability and willingness to impose one's will on others; this includes control over costs and benefits afforded by formalized positions of power). Our use of this term is thus consistent with other work in biology and evolutionary psychology that emphasizes coercive capacity, and diverges from its use in social and personality psychology to refer to assertiveness, control, and social influence that may or may not entail fear and agonism (e.g., Anderson & Kilduff, 2009; Wiggins, 1979; Wiggins, Trapnell, & Phillips, 1988). Readers interested in further discussion of the conceptual definitions of dominance and prestige (as used here and elsewhere) are encouraged to consult Cheng et al. (2013) and Henrich and Gil-White (2001).

community-endorsed recognition achieved by surpassing other in-group members in skill and accomplishments, and emphatically not from superiority in combat or dominating sanctioned enemies from outside the community in formal competitions. By contrast, our assessment of dominance captures the capacity and willingness to induce fear, threat, and compulsion among conspecifics via aggression and intimidation, and not from excelling in a valued domain (such as athletics).

Prestige and Testosterone: The Importance of Longitudinal Change in Large Social Groups

Beyond distinguishing prestige and dominance and their effects on T, this research aims to address two other conceptual gaps in the existing empirical literature, which is limited in its focus on short-term hormonal fluctuations spanning typically minutes or hours in response to status differentiation in the context of dyadic (i.e., two-person) contests. First, on the issue on time-scale, the bulk of existing studies focus on the effects of competition outcomes (a general proxy for relative status) on short-term, ephemeral fluctuations in T in the minutes postchallenge (Carré, Campbell, Lozoya, Goetz, & Welker, 2013; Carré, Putnam, & McCormick, 2009; Elias, 1981; Zilioli & Watson, 2012), or at most in the following day or two (Booth et al., 1989; Mazur & Lamb, 1980; Zilioli & Watson, 2014). By contrast, much prior longitudinal work with nonhuman primates has shown that individuals who experience a rank defeat show depressed T for weeks, sometimes even up to 9 weeks following a profound defeat (Bernstein, Rose, & Gordon, 1974; Rose, Gordon, & Bernstein, 1972). Whether parallel effects are seen in humans over the timescale of weeks or months remains an open and important question, especially given their cumulative and significantly greater influence on long-term neural, cognitive, and behavioral responses compared to acute T fluctuations (Azad, Pitale, Barnes, & Friedman, 2003; Coates, Gurnell, & Sarnyai, 2010; Wright et al., 2012). If affirmative, this would imply that rising or falling in prestige standing can influence long-lasting T change that lead to the emergence of stable, trait-like differences in behavioral profiles.

Second, on the issue of examining the impact of overall status experience, much prior work, whether in the laboratory or field, has focused on the dynamics of T in single shot, one-on-one dyadic competitions (Apicella, Dreber, & Mollerstrom, 2014; Booth et al., 1989; Carré et al., 2009), overlooking the cumulative impact of multiple experiences of winning (or losing) rank competitions across repeated occasions, as well as the overall effects of the numerous prestige-based relationships that an individual possesses with many others on his biology. Evidence indicates that the experience of two consecutive prior losses leads to a greater suppression of T compared to losing a single match in men (Zilioli & Watson, 2014), and that both T and the likelihood of future wins increase after several repeated wins than a single encounter in California mice and swordtail fish (Beaugrand & Goulet, 2000; Oyegbile & Marler, 2005). This suggests that, for our questions of interest, distinguishing between prestige and dominance effects in dyadic versus group-wide rank contests is not merely a matter of methodological differences, but rather represents a key conceptual distinction that emerged more recently in animal behavior (see Chase, Tovey, & Murch, 2003; Dugatkin & Druen, 2004; R. F. Oliveira, McGregor, & Latruffe, 1998). Efforts aimed at understanding the effects of prestige standing on T in humans—a species unique in our ability to monitor and track the reputation and status standing of an exceptionally large set of different partners in our social groups (Mascaro & Csibra, 2012, 2014)—ought to go beyond pairwise, isolated contests by examining the cumulative effects of one's overall rank in a within-group hierarchy. One approach, for instance, might involve sampling all of the dyadic relative prestige ties that an individual possesses with other members in the community, akin to some studies of nonhuman primates in which relative rank is expressed as a function of the total number of conspecifics that the individual outranks. The resultant findings would be crucial for a complete understanding of how an individual's biological system is modulated by his or her full range of prior status experiences within a network of socially embedded dyads.

The Present Study

The current research aims to tackle the conceptual issues outlined above to examine how success in achieving group-wide prestige influences T over an extended timespan. Specifically, we tested the effects of prior prestige experience on subsequent changes in T levels over a 2-month period in a collegiate marching band community of men and women. Participants were asked to nominate who in the community they most respect in terms of musical performance or consider the most musically talented, and to whom they would go for advice related to the band's activities. Following the approach used in prior research for assessing prestige in small-scale groups (Henrich & Broesch, 2011), the degree of recognition one receives from the community in these two closely related domains was used as measures of our two prestige indices (i.e., talent and advice). Nominations of social popularity were also obtained to control for the effects of gaining friendships and alliances, net of any associated prestige gains, on T levels. By focusing on the effects of each member's status ties with all others, rather than a few individuals' assessments of their status or single events of victory (or defeat), this approach captures community-wide recognition across multiple social experiences and affords a more direct test of the cumulative, overall effects of social status on an individual's T.

We predict a positive association between current prestige standing and T increase over time, such that individuals who achieved high ranking in the group's prestige hierarchy in the initial weeks of the organization's formation should show a rising T profile over the subsequent 2-month period. This prediction is based on the empirically robust and well-documented T changes observed following success and defeat in rank contests that contain both prestige and dominance components. In contrast, we expect a weak to null concurrent association between prestige and T in these initial weeks, on the basis that the empirical record shows little robust evidence for the predictive effect of T concentrations (assessed at any single point in time, without accounting for intraindividual change) on eventual rank (Sapolsky, 1991).

Methodologically, we overcome two important shortcomings of existing work on T and social status. The first is that our sample includes 177 individuals from a large-scale community, which represents a major improvement over the use of primarily very small samples of men in prior studies from which concerns with reliability and reproducibility arise (Ioannidis, 2005). Most prior field studies of contest and hormones have tended to examine competing athletes using sample sizes in the range of 6 to 28 men, and in rare occasions 17 to 23 women (Salvador & Costa, 2009; van Anders & Watson, 2006), and often further reduce statistical power by splitting the total sample into two groups of winners and losers for comparison of postgame T levels. This issue persists in many recent field studies (Carré et al., 2009; Edwards, Wetzel, & Wyner, 2006; Ponzi, Muehlenbein, Geary, & Flinn, 2016; Ponzi, Zilioli, Mehta, Maslov, & Watson, 2016). Among other factors, the inherent number of contestants involved in the sport and the diurnal rhythm of T—which imposes restrictions on the time of data collection (generally to the afternoon) to minimize interindividual diurnal variability—generate substantial practical challenges for conducting high-powered field studies. Although most laboratory experiments employ somewhat larger samples (especially several recent ones; Apicella et al., 2014; Carré et al., 2013), concerns with sample size, which average roughly 40 or so men (20 in the win or loss condition, respectively), are still abound (Salvador & Costa, 2009; Zilioli & Watson, 2012).

A second shortcoming in prior studies, briefly mentioned above, involves the disproportionate empirical focus on men, which raises questions about how status-related T responses operate in women (van Anders & Watson, 2006). In the current study, our sample includes a roughly equal gender split of 83 men and 94 women, enabling us to test whether T changes in response to prestige experiences operate similarly in both genders. In contrast to the well-documented effect of differential T responses to winning and losing in men, results are mixed in the few studies that tested women. Although the bulk of these studies find no evidence that women's T responds to rank contests (Archer, 2006; Carré et al., 2013; Mazur & Booth, 1998; Stanton & Schultheiss, 2007), several others suggest competition-dependent hormone changes (Bateup, Booth, Shirtcliff, & Granger, 2002; Jiménez, Aguilar, & Alvero-Cruz, 2012; van Anders, Steiger, & Goldey, 2015; though these studies are similarly limited by their use of small samples of 15–23 women), whereas a few others indicate a significant net rise in losers, a reversed pattern from that seen in men (Zilioli, Mehta, & Watson, 2014). Given these highly mixed results, coupled with the low power in many of these studies, whether women exhibit endocrine changes in response to rank contests remains to be empirically established. Conceptually, gender differences in T responses to competition are perhaps to be expected given sexual dimorphism in the relevant physiological mechanisms (Granger, Shirtcliff, Booth, Kivlighan, & Schwartz, 2004; Stanton, 2011).

Method

Participants

Two hundred twenty marching band members who were undergraduate students enrolled in a large public university in the United States consented to participate in the present study (72% of all 306 active marching band members). Following the standard multiinformant complete network approach, we obtained nomination data for the full network from all participating band members (Wasserman & Faust, 1994). However, of these band members, 43 failed to provide both network nomination data and at least one saliva sample, leaving us with 177 participants (53.11% women) in the final sample for the present study. They ranged in age from 18 to 30 years ($M = 19.47$; $SD = 1.53$; three participants did not report) and had completed anywhere from one to six band seasons (including the present one; $M = 2.18$, $SD = 1.19$; seven participants did not report). Participants' demographic observables are summarized in the electronic supplemental material, Table S1.

The semiprofessional community studied here has received numerous recognitions and prestigious awards, and is among the top collegiate marching band organizations in the United States. On a weekly basis, band members participate in four practice sessions that total in 8–12 hr of rehearsal time, and an additional 6–10 hr of performance. These structured meetings create the context for extensive interactions among members of the community, who additionally spend substantial time interacting outside of these hours on their own time. Because of their close-knit nature, members are likely to have substantial knowledge and recognition about each other's reputations, which can in turn shape and respond to individuals' social relationships and biological systems. For these reasons, this organization is particularly well suited for our research goal aimed at exploring the association between success or prestige and changes in T in naturalistic groups.

Procedure

The data reported here were collected at the end of September and the end of November 2013, respectively, which corresponds to roughly 6 and 16 weeks into the then current band season. Hereafter, we refer to these sampling occasions as Time 1 and Time 2. At Time 1, participants completed a demographic survey online. Participants received a personalized e-mail with instructions to log in to an online survey using a unique username and password assigned by the experimenters. In addition to reporting their demographic details, participants completed inventories concerning their personality, health and well-being, and motivations for participating in band—though these measures were collected for an unrelated purpose and not examined here. This online survey was completed 1 week prior to an in-person session during which salivary samples were collected.

During the in-person assessment session, held between 3 and 6 p.m., participants were asked to provide two saliva samples simultaneously as a group, once before and once after the band rehearsal. This salivary sampling protocol was intended to provide a more robust measurement of HPG axis activity during a time at which individuals were socially engaged with the community, increasing the mental salience of their social context and past status experiences (e.g., Gunnar, Sebanc, Tout, Donzella, & van Dulmen, 2003). Moreover, because of the natural HPG axis diurnal pattern (Nelson, 2011), we collected these salivary samples in the afternoon (3–6 p.m.) when the slope of diurnal decline is at its shallowest point to minimize the influence from the diurnal rhythm. Following the band rehearsal, participants also completed social network measures, a peer nominations inventory, and a health questionnaire (unrelated to the present study). These data were collected as part of a larger project on social relationships and hormones (Kornienko, Schaefer, Weren, Hill, & Granger, 2016).[3] All procedures were approved by the university's Office of Research Integrity and Assurance. Our key measures are discussed below in turn.

Measures

Demographic measures. At Time 1, participants responded to an online demographic survey during the 1-week prior to the in-person session, in which they reported their age, gender, ethnicity, and prior experience in college-level marching band participation (number of band seasons, including the current). In addition, we collected information on band section leadership for all participants from the marching band's management (see Table S1).

Prestige measures. We surveyed band members' perceptions of who in the community were considered to be the most successful, skilled, or respected in terms of their musical performance at both in-person sessions. Following existing work on prestige in naturalistic groups (Henrich & Broesch, 2011), these nominations were obtained in two ways. First, we elicited sociometric nominations for perceptions of talent by asking 'who are the most respected or musically talented band members'. Second, we elicited advice nominations by asking 'to whom do you go to for marching band-related advice, information, and help.'[4] Importantly, perceptions in these two prestige-relevant domains—talent and advice—are not only conceptually but also empirically distinct from dominance. Prior work has shown that they are uniquely and strongly associated with overall perceived prestige, but not dominance (Cheng et al., 2010). This provides a basis for disentangling the two forms of status, and ensures that our results capture the effects of prestige and not dominance. To facilitate both sets of nominations, we prepared an alphabetized roster containing names and identification code for all band members who were participating in the study. This roster was presented to participants, who were asked to respond to each question by listing the identification code of as many and as few band members as they wish. Participants readily nominated between zero and 20 talented individuals and advisors, respectively. Nomination data were arranged in a binary matrix, where a directed nomination from individual i to individual j was coded as 1 if i nominated j as one of most talented or sought for advice, and 0 otherwise.

These coded responses were used to construct two indices of prestige, which serve as our two key predictor variables for the analyses below. Specifically, we tallied up the number of times each individual was nominated as talented, and use this count as our measure of each band member's perceived talent in the community. Similarly, the number of nominations that an individual receives for advice-seeking is used as an index of advice-giving. To address the positive skew in the nomination variables, a natural logarithmic transformation was performed on each (after all zeros are replaced with .00001) and used in all our analyses below.

Dominance measure. A similar nomination procedure was used to construct a distribution of dominance rankings. During the in-person session at Time 1, we additionally asked group members to identify 'individuals who make others do what they want and force others to follow their plans.' Participants nominated between 0 and 38 coercive individuals. We tallied the total number of coercion nominations an individual received, applied a natural logarithmic transformation to reduce skew, and used this variable as a measure of dominance-rank in the band.

Social popularity and friendship measures. Perceptions of who were considered socially popular and who was considered a close friend were also collected during the in-person session at Time 1. For social popularity, respondents were asked 'who are the most popular and most liked by other band members' and used the same method as above to identify as many popular band-mates as they wished. Participants nominated between zero and 20 popular individuals. The tally of the total number of popularity nominations an individual received was used as our measure of popularity in the band. For friendship, respondents nominated who they considered '[their] closest friends with whom [they] spend a lot of time doing different activities and whom [they] can count on when [they] need help," which yielded between zero and 19 friendship nominations. The tally of the total number of friendship nominations an individual received (in-coming ties) and the number of friendship nominations they made (out-going ties) were used as two separate (though conceptually related) measures for the size of one's friendship network. As in our other nomination measures described above, a natural logarithmic transformation was applied to all three of these variables to reduce skew.

Testosterone assays. At the in-person session at both Time 1 and Time 2, which always occurred between 3 and 6 p.m., participants provided two whole saliva samples via passive drool into a 2 mL cryogenic vial once before and once after the band rehearsal, generating 4 samples per participant. Samples were collected from every participant simultaneously and then immediately placed on ice and transferred to the laboratory where they were stored frozen at −80°C until assay. Samples were assayed in duplicate for salivary T using commercially available enzyme immunoassays

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[3] The data presented here are part of a larger project examining the links between hormones and social network dynamics in a naturalistic community. The findings reported here complement and extend prior work from members of our team (Kornienko et al., 2016), which focused on how testosterone and cortisol each predict the likelihood of forming and maintaining friendships over time. Here, we sought to explain the effects of prestige-based status (not examined in this prior work) on T calibration. Prestige—operationalized as the degree to which one is recognized as successful, skilled, or respected—is distinct from the acquisition of social networks of friends, though these two concepts are likely to be positively correlated (see electronic supplemental material).

[4] Note that, though similar, these two measures of prestige might be considered distinct. Whereas one generates sociometric data, the other yields social network data, a subtle distinction consistent with prior work. Nominations of perceived talent capture a nominator's (i.e., in social network terminology, an ego's) *perceptions* of a nominee's (i.e., an alter's) traits and characteristics, and is thus nonrelationship-specific—for example, a nominator may deem a nominee prestigious from observing the deference that others pay her (Chudek, Heller, Birch, & Henrich, 2012). By contrast, advice nominations assess whether the nominator reports a *relationship-specific network tie* with the nominee (i.e., the nominator seeks advice from the nominee). In social network analysis terms, only this latter measure constitutes an indegree measure. Despite this nuance, however, the conceptual meaning of the two resultant measures—computed by tallying the total number of nominations an individual receives—are highly similar, in that both capture the degree to which an individual possesses prestige in the community, whether by virtue of being deemed talented or worthy of offering valuable advice. Thus, for simplicity's sake, throughout this article we refer to these two indices of prestige as talent and advice nominations, respectively.

without modifications to the manufacturer's recommended protocols (Salimetrics, Carlsbad, CA). The test volume was 50 μL, and range of sensitivity was from 1.0 to 600 pg/mL. Interassay and intraassay precision (coefficient of variation) were, on average, less than 15% and 10%, respectively.

T concentration from the pre- and postrehearsal samples (collected three hours apart, within the same session) were strongly associated at both Time 1 ($r = .59$, $p < .0001$) and Time 2 ($r = .80$, $p < .0001$). Given the limited reliability of a single salivary sample for hormone assessment (Granger et al., 2012), we derived a more reliable measure of T by aggregating the T concentration of the pre- and postrehearsal samples within a session to capture T at each time point (Dabbs Jr., 1990; Dariotis, Chen, & Granger, 2016).[5] Although these aggregated Time 1 and Time 2 T measures were positively correlated ($r = .77$, $p < .0001$), the degree of association indicates moderate rank-order stability, leaving open the possibility of interindividual variation in magnitude and direction of change. Both variables were then used in our analyses below to examine change in T. Due to absence and late arrivals or departure from band rehearsal, saliva samples were unavailable from one participant at Time 1 (0.01% of $n = 177$) and 13 participants at Time 2 (7.34%), leaving available T change data for 163 participants (75 men, 88 women).

The simultaneous, collective salivary sampling procedure deployed was designed to provide a more robust measurement of HPG axis activity by (a) increasing the saliency of individuals' membership and participation in the local community and social network through sampling in the presence of their peers and the local group (Gunnar et al., 2003) and (b) restricting saliva collection from all participants to the afternoon (3 to 6 p.m.)—a time during which the slope of T diurnal decline is at its shallowest point—to minimize the influence from the diurnal rhythm of T, which, on average, peaks in the morning and declines dramatically before noon and then declines more slowly in the afternoon and evening hours. To minimize the risk of contamination, participants were alerted in the 1 week prior to each in-person session to refrain from consuming alcohol, drugs, or caffeine, and from performing strenuous physical activity 12 hr prior to session. They were also asked to avoid consuming large meals, dairy products, foods with high sugar or acidity, or caffeine, and to avoid brushing teeth 1 hr prior to the session.

Change in testosterone. Following prior work that examined change in T (e.g., Knight & Mehta, 2017; Schultheiss et al., 2005), change in T was computed using residual change scores. Residual change scores were computed using the unstandardized residuals of a regression analysis with Time 1 T as the predictor and Time 2 T as the outcome, and thus reflect differences in Time 2 T that cannot be accounted for by Time 1 T. Positive residual values indicate relatively higher than expected T at Time 2 given Time 1 T, whereas negative residual values indicate a relatively lower than expected T at Time 2 given Time 1 T; together, they serve as an indirect measure of relative rise and fall in T. This approach is employed here because it provides a more precise and statistically powerful test of whether a trait of interest (such as prestige) is associated with change (Cohen, Cohen, West, & Aiken, 2003; Cronbach & Furby, 1970; Oakes & Feldman, 2001; Zimmerman & Williams, 1982). We rely on simple change scores (i.e., Time 2 T − Time 1 T)—an alternative approach to assessing change—as a robustness check (Mazur et al., 2015; Mehta & Josephs, 2006).[6]

Results

Preliminary Analyses

Table 1 displays the descriptive statistics for our key variables, including raw T, change in T, and number of talent, advice, coercion, and popularity nominations. The average band member received 2.89 talent nominations (range = 0–65; *SD* = 8.45) and 3.84 advice nominations (range = 0–48; *SD* = 7.17). This spread observed across individuals in the number of nominations received suggests that, in these prestige-relevant domains, a few individuals receive many more nominations than the rest of the group, and that substantial between-person variation exists in prestige within the community.

Men and women did not differ significantly in the mean number of peer nominations received on talent, $t(175) = 1.41$, $p = .1600$, or advice, $t(175) = .91$, $p = .3665$. A more detailed summary of our nomination variables, and their intercorrelations, are provided in the electronic supplemental material, Tables S2–S8. Notably, as expected, our two measures of prestige—talent and advice nominations received—were positively correlated (in the pooled sample: $r = .51$, $p < .0001$; in men: $r = .51$, $p < .0001$; in women: $r = .50$, $p < .0001$).

Prestige and Change in Testosterone Over Time

We expected that males who are recognized by their community as skilled, talented, and prestigious would show a rising T profile over time, compared with those who receive little or no recognition. In contrast, given the mixed evidence regarding whether women exhibit T changes in response to status changes, we expected a weak to null relationship between prestige and T change among females.

Talent nominations and change in T. We first addressed the effect of talent nomination by examining the association between the number of talent nomination received and relative change in T from Time 1 to Time 2. To test this prediction, we regressed change in T on the main effects of talent nomination and gender (with females coded '1'), as well as the interaction between talent nominations and gender. The full model results are presented in the electronic supplementary material, Table S9. As predicted, a significant interactive effect emerged between gender and talent, indicating a differential effect of talent on degree of T change for males and females [$b = -1.72$, $t(159) = -2.74$, $p = .007$, .95 CI

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[5] Data screening, conducted separately by gender, revealed that one female participant's average of pre- and postrehearsal T at Time 1 was 3 *SD* above the mean for women, so this value was replaced with the value at 3 *SD* above the mean to reduce the potential influence of this extreme case.

[6] Decision rules proposed by Zumbo (1999) for maximizing the reliability of the index of change recommend the use of residual change scores rather than simple difference scores, as was done here, when the ratio of the standard deviation of the measure at Time 1 to the standard deviation at Time 2 ($\frac{SD_{\text{Time 1 T}}}{SD_{\text{Time 2 T}}} = \frac{34.3508}{37.1511} = .9246$) is greater than the correlation between the two measures at the two time points ($r = .4487$), a condition that is satisfied here.

Table 1
Descriptive Statistics for Key Variables

Gender	Variable	*N*	Mean	*SD*
Men	Testosterone at Time 1 (pg/mL)	83	121.21	32.19
	Testosterone at Time 2 (pg/mL)	75	108.15	37.06
	Residual change in testosterone (pg/mL)[a]	75	5.83	34.17
	Raw change in testosterone (pg/mL)[b]	75	−12.74	36.82
	Talent nominations received	83	3.84	11.15
	Advice nominations received	83	4.36	9.19
	Coercion nominations received	83	1.72	5.12
	Popularity nominations received	83	5.58	17.68
	Friendship nominations received	83	6.70	5.78
	Friendship nominations made	83	6.78	4.44
Women	Testosterone at Time 1 (pg/mL)	93	58.62	24.24
	Testosterone at Time 2 (pg/mL)	89	49.39	20.11
	Residual change in testosterone (pg/mL)[a]	88	−4.97	16.17
	Raw change in testosterone (pg/mL)[b]	88	−8.12	18.43
	Talent nominations received	94	2.05	4.89
	Advice nominations received	94	3.38	4.73
	Coercion nominations received	94	1.26	3.28
	Popularity nominations received	94	2.94	5.95
	Friendship nominations received	94	6.89	4.25
	Friendship nominations made	94	6.82	5.01

[a] Residual change in Testosterone (T) was indexed using unstandardized residuals from the regression of Time 2 T on Time 1 T. [b] Raw change in T was computed by subtracting Time 1 T from Time 2 T (i.e., Time 2 T − Time 1 T).

(−2.96, −.48)]. Confirming our predictions, simple effects for each gender indicated a significant positive association between talent and greater T change in men relative to peers, but not in women. Our model estimated 1.74 pg/mL higher than expected T per additional logged nomination in males [$t(159) = 3.79$, $p < .001$, .95 CI (.83, 2.65)]. By contrast, however, females showed a small and nonsignificant relative change of .02 pg/mL per additional logged nomination [$t(159) = .04$, $p = .970$, .95 CI (−.83, .86)], revealing a lack of association between prestige and degree of T change over the 2-month period. Taken together, this model, which explains roughly 12% of the variance in T change, suggests that, for men, going from 0 (the bottom 50th percentile in the community in terms of talent nominations received) to 5 talent nominations (the 90th percentile) predicts a T level that is roughly 22.81 pg/mL higher than expected (given Time 1 T) at the end of the 2-month period. These simple effects are illustrated in the top panel of Figure 1, which plots the mean change in T relative to the community as a function of talent nominations for men and women.

Advice nominations and change in T. The same pattern of results as above was obtained using advice nominations, our second index of prestige. Similar to our analyses above for talent nominations, we regressed change in T on the main effects of prestige nomination and gender (with females again coded ‘1’), and the interaction between advice nominations and gender. The full model results are presented in the electronic supplementary material, Table S10. Combined, these predictors explain approximately 11% of the variance in T change. Consistent with the results for talent nominations, we found a significant interactive effect between gender and advice in predicting relative T change [$b = -1.98$, $t(159) = -2.71$, $p = .007$, .95 CI (−3.42, −.54)]. As predicted, simple effects showed a significant positive predictive effect of advice on level of T change in men but a null effect in women. In men, each logged advice nomination predicts a T change that is approximately 1.86 pg/mL higher than expected given T at Time 1 [$t(159) = 3.47$, $p = .001$, .95 CI (.80, 2.92)]. Women, by contrast, showed a small and nonsignificant relative *de*crease of .12 pg/mL per additional logged advice nomination [$t(159) = -.24$, $p = .812$, .95 CI (−1.10, .86)], and again, on average, showed a relatively lower than expected T level at Time 2 irrespective of their prestige. These results suggest that, for men, going from 0 (the bottom 25th percentile in the community in terms of advice nominations received) to 10 talent nominations

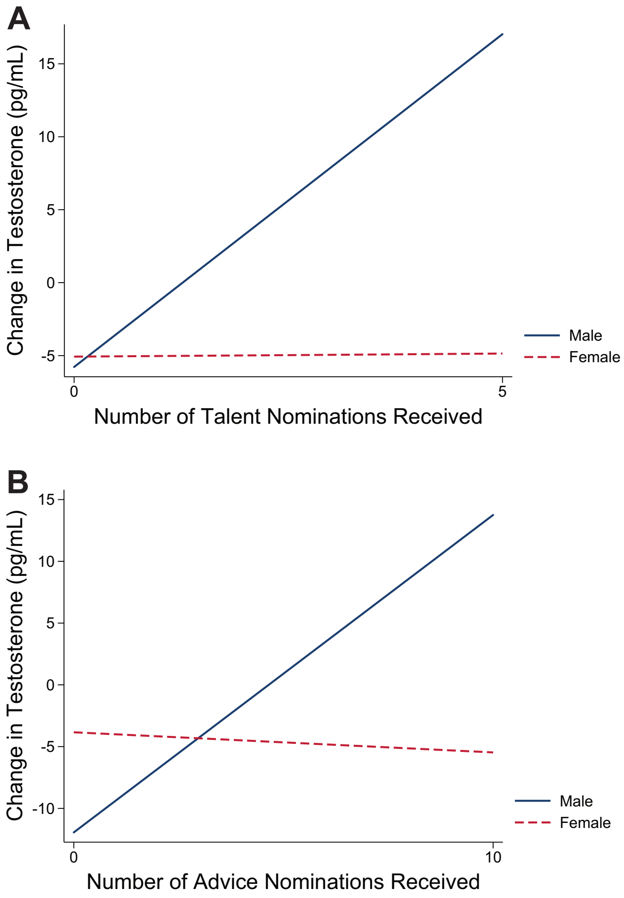

Figure 1. Simple slopes depicting predicted relative change in testosterone (T) as a function of the number of talent nominations (panel A) and advice nominations (panel B) received for men and women. These lines of best fit emphasize a relatively greater increase in T among men with greater prestige in the community, and no prestige-dependent change among women. The associations depicted are based on the natural logarithm of nominations. However, for ease of interpretation, the *x* axis displays the raw number of nominations received: ‘0’ and ‘5’ or ‘10.’ Zero nomination corresponds to the bottom 50th percentile for talent nominations, and the bottom 25th percentile for advice nomination. Five and 10 nominations correspond to the 90th percentile for talent and advice nominations, respectively. Relative change in T was indexed using residual change scores (i.e., unstandardized residuals of Time 2 T regressed on Time 1 T), which capture a person’s degree of change *relative* to other individuals (rather than a person’s *absolute* change). See the online article for the color version of this figure.

(the 90th percentile) predicts a T level that is roughly 25.70 pg/mL higher than expected at the end of the 2-month period given their Time 1 T. These simple effects are illustrated in the bottom panel of Figure 1.

Together, results across these two indices of prestige converge to indicate that highly prestigious men exhibit higher T two months later compared with their low-ranking counterparts (controlling for any difference in Time 1 T). This pattern of greater T change among more prestigious men is consistent with the notion that gaining high rank in a prestige hierarchy is associated with greater T modulation.

Raw change in T. While our approach above (based on the residual score measure of change) provides a precise and statistically powerful means for testing the association between prestige and T change, we next sought to complement these results with the raw difference measure of change (Time 2 T minus Time 1 T) and to examine convergence of results across approaches. This raw change index correlates very strongly with the residual change index ($r = .93, p < .0001$), as expected. It is also important to note that these two measures of change from two-wave data address complementing but distinct questions regarding change. In the simplest form, whereas residual scores investigate whether the more prestigious individuals show greater change in T from Time 1 to Time 2 *relative* to less prestigious individuals (while holding constant any initial differences in Time 1 T), raw difference scores compare average actual change in T between individuals with higher and lower prestige (Hand & Taylor, 1987; see electronic supplemental material for further discussion), though note that our analyses here treat prestige as a continuous, rather than binary, predictor variable. Thus, despite the residual scores results above demonstrating greater Time 2 T (controlling for Time 1 T) among highly prestigious individuals (and hence greater change associated with higher prestige), more definitive conclusions regarding the precise pattern of T change (such as the hypothesized rise in T among the most prestigious, and a drop in T among the least prestigious) require considering raw change in combination with residual change.

To illustrate the observed trends, Figure 2 shows the mean raw change in T in men as a function of discretized categories of talent and advice nominations. Men with zero nomination, indicating low prestige in the community, show a negative change in T from Time 1 to Time 2, consistent with a declining T profile. As prestige standing increases, from 0 to 1 to 4 nominations and then to 5 or more nominations, there is a dramatic stepwise shift from a negative change to positive change, such that the most highly ranked men show a rising T profile across time.

To formally investigate the differential T change profiles visible in Figure 2, we reran our baseline regression model (and alternative specifications) using raw change. The pattern of results remained significant and consistent with our primary findings based on residual change presented above (see electronic supplemental material, Tables S19–S22). Simple effects in each model consistently reveal an association between prestige and raw T increase in men, estimating an absolute T increase of roughly 1.61 pg/mL per additional logged talent nomination and 1.65 pg/mL per additional logged advice nomination, and a small and nonsignificant effect among women.

Together, these results using both residual and raw measures of change converge—giving us confidence in the robust nature of our results. Our key finding is that not only do prestigious men show greater positive increase in T over the subsequent two months relative to their less prestigious peers (as shown by residual change scores), but the more precise pattern is such that the most prestigious men show a rise in T over time whereas the least prestigious

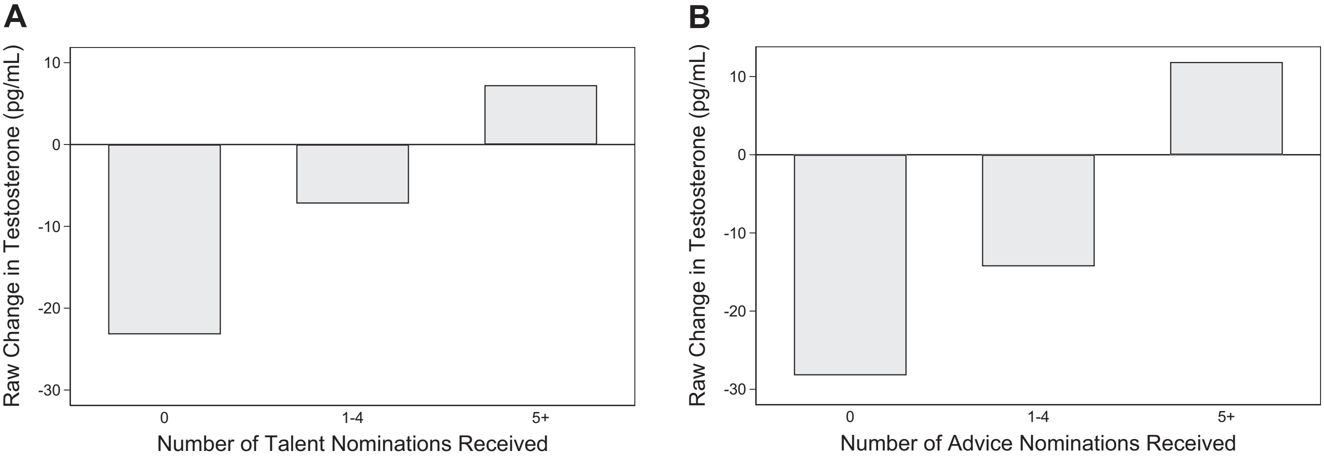

Figure 2. Bar graphs depicting mean raw change in testosterone (T; indexed using simple change scores: Time 2 T minus Time 1 T) in men as a function of discretized categories of raw nomination counts for talent (panel A) and advice (panel B). Intuitively, positive values indicate an absolute increase in T from Time 1 to Time 2, and negative values indicate an absolute decline. Visual inspection suggests that men with the highest prestige ranks in the community (who received five or more talent or advice nominations) show a rise in T over time, whereas men with least prestige (who received zero talent or advice nominations) show a drop in T over time. Comparisons of these means (reported in the electronic supplemental material) confirm that these groups of men—who occupy the highest and lowest strata of a prestige-based status hierarchy—exhibit significantly different mean raw change in T across time.

men show a declining T profile (as shown by raw change scores). These patterns are consistent with the idea that experiences of status calibrate the up- and down-regulation of testosterone in a manner that adaptively guides future status-seeking efforts.

Prestige and Concurrent Testosterone

We expected prestige to be either weakly or not at all associated with concurrent T concentrations at Time 1 in both men and women. In these initial weeks of group formation, it is unlikely that individuals have accumulated sufficient opportunities to receive and observe deference paid toward themselves, and to fully sort out their prestige standing in this large community. Consequently, endocrine modulations in response to local rank dynamics at Time 1 are likely minimal relative to two months later at Time 2 (see electronic supplemental material for an expanded discussion). As expected, neither talent nor advice nominations was significantly associated with Time 1 T (in the pooled sample, *r*s = .05 and .08, *p*s = .4979 and .2680, respectively; in men, *r*s = .13 and .16, *p*s = .2441 and .1536, respectively; in women, *r*s = −.11 and .05, *p*s = .3140 and .6255, respectively; see Table S8), though note the weak positive trend in men (see electronic supplemental material for discussion).

Robustness Checks

To further explore the robustness of our T change findings, we present four sets of additional analyses in the electronic supplementary material, which we briefly summarize here. First, we reran the baseline models reported above for both talent and advice nominations as predictors and additionally included a number of controls: dominance, social popularity, friendship ties (both incoming and out-going), age, ethnicity, prior marching band experience (in years, with ‘1’ meaning first season and no prior experience), and section leader status. In particular, dominance was controlled for to ascertain that the observed pattern of rising T in prestigious individuals is not due to the same individuals being highly dominant (i.e., to disentangle the effects of prestige from dominance processes). Social popularity and friendship ties were controlled for to address the concern that the observed link between prestige and T change may be driven by the possibility that prestigious men also enjoy greater social popularity, a position that might alter their hormone profiles (Kornienko, Clemans, Out, & Granger, 2013). Results from these models, displayed in Models 3 to 5 in Tables S9 and S10 (residual change as outcome), and in Tables S19 and S21 (raw change as outcome), show that our primary findings are robust to these alternative explanations; the inclusion of coercion and popularity nominations (and their interactions with gender) as predictor variables does not change the coefficients and significance of talent and advice (and their interactions with gender).[7] Similarly, in the other alternative specifications that include gender, ethnicity (dummy coded, with Caucasians as the reference group), prior marching band experience, and section leader status as controls, the coefficients on talent and advice (and their interactions with gender) remain largely unchanged and highly significant—see Models 6 to 9 in Tables S9, S10, S19, and S21.

Second, across all of these alternative specifications, simple effects for each gender show that the positive effect of prestige on relative T change among men increase varies little (increasing, if anything, in these specifications with controls)—ranging from an increase of 1.71 to 1.91 pg/mL per log talent nomination, and 1.78 to 2.28 pg/mL per log advice nomination—and remains sizable and significant (see the electronic supplemental material, Tables S11 and S12). Also consistent with the baseline model, no significant association was found among women in any of these other specifications. These simple effects reconfirm the above findings of an association between prestige and T increase in men and a null effect in women.

Third, the above described results that compare absolute T change (indexed by simple difference scores) across discrete, ordinal categories of prestige nomination counts are replicated using the residual change measure. On average, men who received zero nomination experienced a relatively smaller change in T from Time 1 to Time 2 (*M* = −5.40 pg/mL for talent; *M* = −11.42 pg/mL for advice), whereas men who were atop the community’s prestige hierarchy—defined as being nominated 5 or more times, which corresponds to the top 10 percentile at the group level—showed a relatively greater positive increase in T (*M* = 27.98 pg/mL for talent; *M* = 31.67 pg/mL for advice; see Figures S3 and S4, which parallel Figure 2 Panels A and B). Importantly, these results based on raw, nontransformed nomination data, which are consistent across both measures of change, clarify the T change patterns for group members, by demonstrating that men who lack recognition (i.e., receive 0 or several nominations) at the community level experience either a decline or little change in T. This pattern contrasts sharply with the sizable rise in T seen in widely recognized men. Moreover, additional analyses using robust regressions indicate that our results are robust to statistically accounting for the influence of potential outliers (see electronic supplemental material).

Fourth, an alternative approach to assess prestige in the community involves casting the total nominations received by each individual into actual rankings, wherein the most frequently nominated member of the community is ranked first. This approach, frequently deployed in work in biology and primatology to quantitatively encapsulate the dominance relationships among members of wild baboon and chimpanzee social groups (Alberts & Altmann, 1995; Sapolsky, 1983), more directly captures the concept of a linear status hierarchy (a “pecking order”). The above described results all hold using these ranking measures. Our baseline model estimates that 10-rank increase in talent and advice is associated with a higher than expected T increase of roughly 1.74 to 2.25 pg/mL (residual change), and an absolute increase of 1.39 to 2.07 pg/mL (raw change; see Table S23 in electronic supplemental material). Overall, these supplemental analyses indicate that the effect of prestige on T change is robust to these checks.

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[7] In a separate series of regression models in which all prestige predictors were dropped, we found that, in fact, neither dominance nor social popularity or friendships predict relative T change (see Tables S15 to S18). These results provide clear evidence that our observed associations between prestige and T change are not attributable to endocrine responses triggered by experiences of dominance or social popularity.

Discussion

The present results provide the first evidence that prestige standing in the initial weeks of a large-scale social community's formation predicts subsequent, long-term changes in T. Men who held the highest ranks in the group's prestige hierarchy showed a rising T profile over the subsequent two months. This pattern of results converged across our two measures of prestige involving talent and advice nominations, which capture group-wide perceptions of who in this community were considered the most musically talented or ideal models to target for advice and learning. No parallel effects, however, were seen in women. Our ancillary analyses indicate that this social modulation effect arises only from the achievement and experience of prestige-based status, and not merely from dominance-based status, social popularity, or friendship network dynamics (Kornienko, Clemans, Out, & Granger, 2014; Kornienko et al., 2016), and does not vary by level of cortisol concentration (see electronic supplemental material). Overall, these findings converge with existing evidence from laboratory and field studies on rapid surges in circulating T occurring minutes in response to changes in social status (R. F. Oliveira, 2004), and supports the general notion that T functions as a physiological mediator by adaptively fine-tuning future competitive behavior to prior social experience and context to increase individual fitness.

Our study makes several novel contributions to the empirical enterprise on social status and T. First, to our knowledge this is the first study to apply the distinction between prestige (i.e., respect and admiration) and dominance (i.e., force and coercion) to the study of how the outcomes of prestige competitions influence hormones. The existing empirical work on hormones treats status as a uni-dimensional construct, leading to the conflation of the effects of prestige and dominance processes on T. Unambiguously disentangling these two dimensions may explain the often mixed and confusing results, and, importantly, generate new insights into the biological basis of prestige hierarchies—a key feature of group living that has been described as a human universal unique to our species (Brown, 1991). Second, our longitudinal study extends the primary focus in existing work on transient, short-term T changes to show that gaining prestige predicts elevated T over the timescale of months in men. Third, our inclusion of a large sample of men and women within the same study—a rare but much needed approach for addressing address the small sample issue that plagues this literature—allows us to reliably test and detect the effects of prestige status on T in men but not women. Notably, there is general consensus among scholars regarding the importance of these three conceptual and methodological advancements. As emphasized in a recent review of the extensive empirical literature on social status and T (Hamilton, Carré, Mehta, Olmstead, & Whitaker, 2015), these three issues (nondominant forms of status, longitudinal effects, and large samples of both sex using the same design) are identified as among the most crucial challenges to which future work on T should attend (Salvador & Costa, 2009; van Anders & Watson, 2006).

Fourth, our results, which are based on summaries of individuals' asymmetrical social relationships with up to roughly 180 people in the community, capture the effects of overall standing in a group-wide prestige hierarchy. This focus on within-group hierarchies contrasts with and adds to existing work that has primarily focused on the outcome of dyadic, pairwise contests (e.g., winner vs. loser) in an effort to simulate the social experience of high- and low-status (Josephs et al., 2006; Mehta & Josephs, 2006; Zilioli et al., 2014; Zilioli & Watson, 2012). These dyadic studies abstract from the complex and numerous social ties that individuals possess in the real world, and fall short of fully tracking and assessing the total influence of one's status experiences on hormones. Our results, on the other hand, derive from actual (rather than simulated) experiences of prestige in a large group, and thus extend the scope of these existing lines of research.

Finally, our focus on a naturalistic large-scale community bridges work from the laboratory to the field and adds to existing laboratory-experimental evidence, which involves primarily rigged competitions (Gladue et al., 1989; McCaul et al., 1992; Zilioli & Watson, 2012, 2014), by providing more socioecologically valid evidence (Roney & Higham, 2017).Other recent work in line with our naturalistic approach similarly suggests that assessing behavioral endocrinology in groups and networks provides an additional valuable tool for understanding the dynamics of T and other social hormones (Kornienko et al., 2013, 2014, 2016; Ponzi, Muehlenbein, et al., 2016; Ponzi, Zilioli, et al., 2016).

When considered together, these methodological elements converge with insights and recommendations from the latest meta-analysis of studies from the last 35 years addressing how competitive outcomes influence T changes in humans (Geniole et al., 2017). Beyond supplying clear evidence that wins and losses modulate T responses, conclusions from this analysis offer at least three crucial practical considerations for the fruitful study of the interplay between status and T responses: the use of (a) field studies involving real contests (in contrast to laboratory-contrived contests), where the effect of interest is most robust (and almost 6 times stronger than in the laboratory); (b) large samples of men and women to study sex-specific effects, given that currently the effect appears to be reliably found only in men; and (c) substantially larger samples to increase statistical power, given that, of the 62 effect sizes examined, the sample sizes ($N_{\text{average}} = 41.55$, $SD = 26.54$; min = 7, max = 113) and statistical power (average power = .30) are, as the researchers note, woefully inadequate. Of note, in our study the use of a real social group in the field and the examination of T changes in large separate subgroups of men and women accounts for all of these concerns. Compared with this suite of prior studies, our final sample of 163 participants is 4 times larger than the average study, and 1.5 times larger than the highest-powered study. We believe that these aspects of our research design make stronger conclusions of our findings possible.

It is only through these multiple converging lines of evidence generated from different methodological approaches in different competitive contexts that we can develop a robust and complete understanding of the complex interplay between T and social status. Below, we briefly outline the key theoretical implications of our findings and avenues and opportunities for future research.

Theoretical Implications

The social modulation of T. These results add to and complement emerging work demonstrating how androgens respond to current social ecological conditions in male vertebrate species ranging from fish to mice to rhesus macaques (Bernstein, 1981; Lloyd, 1971; R. F. Oliveira, Lopes, Carneiro, & Canário, 2001;

Wingfield et al., 1990). The existing work on humans (and other mammalian species) reveals that T fluctuates in contexts directly (e.g., interacting with a potential mate, parenting) or indirectly (e.g., status competition) relevant to mating effort in a manner consistent with an adaptive, context-sensitive androgenic system (Wingfield et al., 1990). For example, evidence on humans suggests that T rises rapidly in response to the presence of potential mates (López, Hay, & Conklin, 2009; Miller & Maner, 2010; Roney, Lukaszewski, & Simmons, 2007), the anticipation of competition (Archer, 2006; Mazur & Booth, 1998; R. F. Oliveira et al., 2001; Wingfield & Wada, 1989), the prior experience of victory in contests (Booth et al., 1989; Carré & Putnam, 2010; Josephs et al., 2006), but by contrast, T declines in accordance with parenting effort (Gettler, McDade, Feranil, & Kuzawa, 2011; Storey, Walsh, Quinton, & Wynne-Edwards, 2000).

Extending these existing lines of work, our results show that experiences of prestige—receiving respect and deference from coalitional members, which other work has shown to enhance mating and reproductive success (Snyder et al., 2008; von Rueden et al., 2011)—in a social group with cooperative goals leads to increases in T in men. By contrast, men who receive little deference experience a decline or no change in T over time—a pattern consistent with the functional significance of socially induced T responses. However, it is important to note that this pattern of reactivity is not uniformly observed across all forms of social success. As we show here, merely achieving an expansive friendship network and social popularity among group members (net of gains in prestige resulting from these social ties and allies), does not predict increased T. This finding is in line with theory and highlights the theorized function of T in selectively mediating competitive interactions that give rise to differential status.

Testosterone and prestige. By drawing novel connections between T and prestige status (distinguished from dominance status), our findings, combined with current perspectives regarding the functional significance of socially modulated androgen levels, opens up the theoretical possibility that T coordinates prestige processes by responding to the individual's current social experience and propelling future androgen-dependent cognitions and behaviors. To see the adaptive value of socially modulated androgen levels in prestige competitions, consider a new entrant to a chess club who aspires to ascend the prestige hierarchy to become an admired and emulated group member. Despite his exceptional talent and skill in soccer (and substantial prestige among his soccer peers), he lacks skills and success in chess that commands respect among this new group, including the ability to plan, strategize, recognize patterns. As a result, he's able to attract very few deferential followers who would willingly grant him prestige in the chess club. Moreover, immediate efforts aimed at elevating his prestige standing is difficult and would be met with little success, given that rising in prestige ranks derives from a substantial improvement in his chess skill and knowledge and thus cannot be quickly achieved. Consequently, a mechanism of plasticity that suppresses his status motivation and behavioral patterns in accordance with his current experience of low prestige in chess, including muting his motivation to demonstrate his (lack) of skills and status displays and other claims to status, would minimize the costs associated with these attempts (e.g., challenging a more skilled individual) and thus promote a net gain in fitness. As suggested by our results, his T release—influenced by the experience of low-prestige—is likely to be suppressed, creating a profile of decreased endogenous T relative to the time of entry. On the other hand, consider another new entrant who excels in chess and consequently receives extensive prestige-based deference. Unlike the other entrant, he ought to respond with an amplified motivation toward further sustaining and improving his prestige. We believe our findings are best interpreted in light of the notion that T responses provide such a mechanism of behavioral plasticity. By down- or up-regulating T as a function of past prestige standing, these T changes either inhibit otherwise ill-suited prestige-seeking efforts when the current conditions are not favorable for improving one's standing, or heighten these androgen-dependent prestige motivations, cognitions, and behaviors under favorable conditions.

This theoretical connection between prestige and T responsivity is important because it suggests that T may act as a physiological mediator in a more diverse range of competitive situations than previously thought, including prestige-based competitions predicated on skill, achievement, and perceived merit. Here, men who effectively gained more prestige—by earning substantial respect and recognition for their skills and achievement in this marching band community—experience an increase in T, even though this form of rank involves neither physical or psychological force or threat (dominance), nor superiority over a sanctioned enemy or competitor. Thus, by establishing that T fluctuates in accordance with prestige-based rank outcomes, these results suggest that T appears to be a physiological substrate that adaptively prepares and propels behavior in competitive contexts based entirely on skill and earned merit to facilitate the acquiring, sustaining, and signaling of prestige-based status. This contrasts with and expands upon the prevailing view of T as a hormone that primarily regulates agonism (aggression, intimidation, force, and fear) and facilitate the emergence of dominance asymmetries in humans and other species (Gleason, Fuxjager, Oyegbile, & Marler, 2009). Taken together, we believe that these existing empirical patterns are best interpreted to indicate that prestige contests are coordinated by T, which is functionally designed to mentally and physically prepare individuals to optimally extract social benefit from status opportunities and enhance fitness, albeit via distinct pathways.

Though future work is needed to fully sort out precisely how elevated T levels coordinate adaptive responses geared toward the attainment of prestige (i.e., to unravel the suite of motivational, affective, behavioral mechanisms through which elevated T increases the probability of gaining more prestige), other parts of this theoretical notion have begun to garner some preliminary empirical support. The strongest support comes from recent evidence indicating that T may increase prosociality—a key ingredient to enhancing one's group-wide prestige, because supplying public goods is a highly effective means to broadcast one's abilities and in turn attract a large coterie of deferential followers (Cheng et al., 2010; Hardy & Van Vugt, 2006; Henrich et al., 2015; Henrich & Gil-White, 2001; Willer, 2009). These studies show that testosterone administration increases cooperation, fairness, and reciprocity in economic games, especially when status concerns are made salient (such as in interactions with members of one's coalition; Boksem et al., 2013; Eisenegger et al., 2010; van Honk, Montoya, Bos, van Vugt, & Terburg, 2012). Although more evidence is needed to draw firm conclusions, these results offer some preliminary support to the notion that elevated T may propel motivational, cognitive, and behavioral tendencies that influence success in prestige contests, while simultaneously qualifying the intuited and straightforward one-to-one link between T and aggression (Boksem et al., 2013; Casto & Edwards, 2016; Edwards et al., 2006; Eisenegger et al., 2010).

Is elevated testosterone an endocrine profile that confers high-rank? Despite our finding that T responds to success and defeat in prestige contests, we found no strong evidence that T confers prestige. At Time 1 (that is, in the initial weeks of the group's formation) the observed associations between T and our measures of prestige (*r*s = .13 for talent and .16 for advice), despite being in the positive direction, were only modest and did not reach conventional levels of significance. However, a potential concern in interpreting this null effect is that it may be an artifact of our sample size, which limits the statistical power available to detect small effects. Future designs should use larger sample sizes to derive stronger conclusions. It is worth noting, however, that the null association obtained here is not entirely surprising, and may in fact be anticipated by existing lines of evidence from diverse species, which have similarly produced weak or null associations between T and various forms of social rank (Akinola et al., 2016; Mazur et al., 2015; van der Meij et al., 2016; see electronic supplemental material). Together, this body of findings challenges the false, but widely believed, folk notion that there exists a single, robust physiological determinant (or a set of determinants) of rank in primates (Eisenegger et al., 2010; Whitten, 2000). Instead, endocrine profiles, such as high T, may best be understood as markers of behavioral styles and personality (Sapolsky, 1991). It may be the case that hormones and traits predispose individuals toward certain behavioral strategies (e.g., greater competitiveness, status motivation, risk-taking) that probabilistically influence rank relationships. However, as emphasized by theorists (Bernstein, 1981; R. F. Oliveira et al., 2016), because rank asymmetries are complex behavioral outcomes that arise from mutual relationships with other individuals (rather than from absolute attributes of any single individual) and are, in some cases, influenced by local social mechanisms (e.g., norms that determine legitimate avenues of status), these markers may predict but do not alone determine social outcomes.

Longitudinal changes in T. Understanding the effects of social status (whether derived from prestige or dominance) on an organism's psychology requires considering both how specific instances of social victory and defeat spur immediate transient physiological changes and how these microlevel changes aggregate up to produce long-term patterns to ultimately generate stable, trait-like physiological profiles. Whereas most existing studies have delineated the former, our study fills the important gap on the longitudinal side by demonstrating the long-lasting effects of achieving prestige on circulating T over a timescale spanning months. Notable in this sample is that elevated T levels result from, rather than precede, the achievement of high rank, given our results showing that individuals who ended up achieving higher prestige did not simply begin with higher endogenous T at Time 1. Rather, receiving deference from members in the community is associated with an increase in T over the subsequent months. One important methodological limitation here, however, is that, as in many longitudinal field studies, unexamined confounding factors specific to one or both of the assessment time points might give rise to the association we observe between prestige and T change across time. This may include, for example, a greater competitive mindset at our second time point (perhaps arising due to an upcoming marching performance), greater physical exertion in one of the rehearsals, increased cooperativeness or engagement with the community from strengthened social bonds and relationships, among other possibilities. Future designs should attempt to assess and explore the influence of these significant band events or experiences that we lack data to address here.

Notably, these patterns are consistent with those long noted among nonhuman primates, for whom both one-off experiences of victory and defeat in dominance contests and current rank order reflecting prior repeated interactions lead to prolonged elevation or suppression of androgens over weeks and sometimes even months (Beehner, Bergman, Cheney, Seyfarth, & Whitten, 2005; Bernstein et al., 1974; Rose et al., 1972). Moreover, the enduring nature of these status-dependent T modulation effects may be in kind similar to the long-term suppressive effects of fatherhood on testosterone (and a "paternal physiology" profile more broadly), which evolved to promote a stable parental care behavioral phenotype designed to facilitate men's bonding, attachment, and long-term commitments to their offspring male (Gettler, 2014).

These repeated, long-lasting changes in T are likely functionally distinct from ephemeral and temporal T fluctuations, because prolonged activation of the androgen system may, over the course of development, instill or create trait-like patterns (Jones, 2006). That is, unlike the transient, one-off spikes or drops in T that are designed to organize phenotypic plasticity by guiding short-term expressions of behavior at the activational level (e.g., competing or backing down in a given interaction), long-term T levels that are shaped by repeated experiences of high or low status may give rise to the emergence of slow, stable interindividual differences in behavioral profiles (e.g., cross-context dominant vs. submissive *types* or proclivities) by structurally rewiring neural circuits (Arnold & Breedlove, 1985; Gilbert, Price, & Allan, 1995; R. F. Oliveira, 2009). This effect of status on testosterone may be particularly important at the organizational level, whereby changes in androgen release during early development may influence life history stage decision-making (e.g., body size, age of first reproduction, reproductive life span, number of offspring, level of parental investment; Beehner et al., 2009; Coates et al., 2009, 2010; Zera & Harshman, 2001).

Of course, to more fully understand the influence of androgens also requires, among other things, explaining the interplay between androgen receptors and social rank, beyond strictly androgen levels. Work on naked mole-rats and cichlid fish suggests that dominance also regulates variation in androgen receptor gene expression (Burmeister, Kailasanath, & Fernald, 2007; Holmes, Goldman, & Forger, 2008), which in turn produces differential sensitivity to androgens and, as a result, influences the behavioral consequences of androgen exposure. This, combined with evidence that changes in social rank can trigger modifications in brain morphology (Holmes et al., 2007), indicates the potential for social experiences to exert extensive influence on neural structures. Whether this extends to other species, including humans, remains to be seen. More broadly, future studies should further probe whether and how an organism's physiological, behavioral, and neural mechanisms respond differently to single-shot and recurring experiences of success or defeat at both activational and organizational levels.

Sex differences in the social modulation of T. In this study we find no evidence that prestige experiences modulate subsequent T responses in women, as it does in men. Though this gender difference is anticipated by existing empirical work, which has typically produced null or highly mixed results for women (Bateup et al., 2002; Carré et al., 2013; Geniole et al., 2017; Jiménez et al., 2012; Mazur & Booth, 1998; T. Oliveira, Gouveia, & Oliveira, 2009; Stanton & Schultheiss, 2007; van Anders & Watson, 2006) and in females of many other species (Koren, Mokady, & Geffen, 2006), this pattern of gender difference deserves further examination. In particular, future research should attend to the details of sex-related measurement issues with salivary testosterone and sexually dimorphic physiological mechanisms, both of which may partially explain the observed sex difference. For example, existing evidence indicates sex differences in salivary testosterone levels and variance, the testosterone serum-saliva association, the association of salivary testosterone with age and pubertal development, and the stability of individual differences in salivary testosterone levels over time (see Granger et al., 2004). Further, animal model studies reveal, for instance, sex differences in testosterone metabolism, testosterone brain uptake, and the metabolic effects of testosterone (Nelson, 2011; Sholl, Goy, & Uno, 1982).

Another possible explanation for the observed null association in women may stem from a measurement issue. Despite the widespread use of the enzyme immunoassays method deployed here to measure salivary T, the accuracy and validity of this approach, especially in women samples, has recently come under debate in the field of salivary bioscience (Welker et al., 2016). Other technical issues have similarly pointed to the possibility of inflated assayed concentrations for both salivary and plasma or serum T in women (and children) samples (Granger et al., 2004; Rosner, Auchus, Azziz, Sluss, & Raff, 2007; Shirtcliff, Granger, & Likos, 2002). These potential issues, if true and applicable, would reduce the sensitivity and accuracy of our measures of T concentrations in women, and might explain why the association between status and T change was obtained in men (for whom T measures are more accurate) but not women in the present study, as well as in many other existing work (Welker et al., 2016). Nevertheless, given the limited and mixed available evidence, further studies directly comparing the T responses of men and women in competitive contexts using high powered designs and improved methods for measuring T are needed to draw any definitive conclusions regarding gender differences.

Concluding Remarks

Competition is a central and defining feature of the lives of social species. In humans, competition over social status and resources is particularly complex and uniquely multidimensional—deriving not solely from dominance, coercion, and intimidation as seen in other primates, but also from prestige based on respect and admiration arising from superior skills, abilities, and perceived merit. The emergence of prestige-based hierarchies in our species might have created selection pressures that favored the coevolution of a suite of fine-tuned psychological, cognitive, and physiological systems designed to generate behavioral plasticity in a manner that optimizes potential gains (and minimizes costs) across a broad range of social relationships and contexts that involve differential prestige. The present investigation, which examines the longitudinal effects of attaining prestige on biological systems in a large-scale naturalistic community, provides initial evidence that, in men, the status-induced modulation of testosterone is one of the biological mechanisms that underlies the establishment and maintenance of prestige hierarchies.

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