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Review article

Human reproductive behavior, life history, and the Challenge Hypothesis: A 30-year review, retrospective and future directions

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ABSTRACT

The Challenge Hypothesis (Wingfield et al., 1990) originally focused on adult male avian testosterone elevated in response to same-sex competition in reproductive contexts. The purpose of the present paper is to demonstrate how the Challenge Hypothesis has shaped ideas about human life histories. We conduct a citation analysis, drawing upon 400 Google Scholar citations in the human literature to identify patterns in this body of scholarship. We cover key factors, such as context and personality traits, that help explain variable testosterone responses such as winning/losing to adult competitive behavior. Findings from studies on courtship and sexual behavior indicate some variation in testosterone responses depending on factors such as motivation. A large body of research indicates that male testosterone levels are often lower in contexts of long-term committed partnerships and nurturant fathering and aligned with variation in male mating and parenting effort. As the Challenge Hypothesis is extended across the life course, DHEA and androstenedione (rather than testosterone) appear more responsive to juvenile male competitive behavior, and during reproductive senescence, baseline male testosterone levels decrease just as male life history allocations show decreased mating effort. We discuss how research on testosterone administration, particularly in older men, provides causal insight into effects of testosterone in humans, and how this "natural experiment" can be viewed in light of the Challenge Hypothesis. We synthesize central concepts and findings, such as an expanded array of costs of testosterone that inform life history tradeoffs between maintenance and reproductive effort, and we conclude with directions for future research.

1. Introduction

The Challenge Hypothesis was mainly developed from data on seasonally breeding, migratory birds (Wingfield et al., 1990). Its reach has extended these past 30 years dramatically, as evidenced by contributions in this special issue. The value of the conceptual framework for capturing male reproductive behavioral profiles has arguably helped make it adaptable to many taxa, including humans. The Challenge Hypothesis advances the idea that male testosterone levels may exhibit a breeding season baseline, above which social stimuli such as male competitors and potential mates elevate testosterone. Conversely, expression of paternal behavior may be associated with decreases in testosterone. While humans may not be seasonal breeders, the Challenge Hypothesis highlights the relevance of male-male competition, sexually receptive females, partnership formation, and paternal behavior in structuring adult male variation in testosterone levels.

Here, we highlight how the Challenge Hypothesis has shaped ideas about human life histories. Among adult males, this entails focusing on male-male competition and aggression, courtship and sexual behavior, partnering dynamics, and parental care. Because several other contributions in this special issue focus on human competition and aggression, we devote less space to that behavioral domain. We adopt a life course perspective to illustrate the relevance of the Challenge Hypothesis, not just for adult male reproductive contexts, but also to prepubertal and aging individuals, too.

2. Human life histories and the Challenge Hypothesis

Human life histories exhibit key, derived characteristics: early weaning, extended childhood, large brains, late puberty, long-term

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reproductive bonds, paternal behavior, and extended post-reproductive lifespan (Clutton-Brock, 2016; Kaplan et al., 2000; Robson and Wood, 2008). These factors can be understood from the perspective of life history theory, for example by considering them in light of intensive social and energetic pressures. According to Hrdy (2009), humans are cooperative breeders, raised by mothers and a flexible network of additional caregivers such as older siblings, fathers, and grandmothers (Hrdy, 2009). Humans occupy an intensive dietary niche made possible by meat-eating, cooking of plant and animal foods, and extraction and processing of other foods. These social and energetic contributions of various caregivers enable weaning offspring at younger ages than otherwise expected, supporting the metabolic costs of large brains, and evidencing slower life history paces to hone the social and ecological knowledge required for social and reproductive success (Bogin, 1999; Kuzawa et al., 2014). The age-specific reproductive benefits and reduced adult extrinsic mortality may contribute to extended lifespans. These views draw upon comparative animal behavioral research, the study of human hunter-gatherers, and the fossil hominin and archaeological record, among other key sources, even if a more in-depth evaluation is beyond the scope of the present paper.

At the same time humans exhibit species-specific life histories, phenotypic plasticity in these and other life history variables is recognized. Among hunter-gatherers and the broader cross-cultural and historical records, humans vary in weaning patterns, social and energetic aspects of child development, timing and processes of pubertal development, courtship and partnering dynamics, forms and patterns in childcare, and patterns in aging (Kaplan et al., 2009; Kelly, 2013; Low, 2015; Marlowe, 2005). We cannot do justice to that variation here, though we highlight some of the ways that variation in social and ecological context influence human testosterone profiles and responses. One way to see that variation is to take an expansive view of human history that recognizes our species' origin in Africa around 300,000 years ago (Hublin et al., 2017). Subsequent population movements and fluctuations led to small amounts of interbreeding with archaic hominins in Africa, and Neanderthals and Denisovans in Eurasia (Sankararaman et al., 2016). The human population may have neared extinction in Africa, shortly before a major dispersal event outside of Africa around 70,000 years ago that would ultimately give rise to the approximately 7.5 billion descendants spread around the globe today. Throughout this global dispersal, human life history parameters responded to adaptive (e.g., learning locally relevant information during childhood) and historic (e.g., cultural inertia in partnering and parenting dynamics) processes (Garfield et al., 2016; Henrich, 2015; Richerson and Boyd, 2005).

Life history theory recognizes that individuals allocate limited time and resources to competing agendas of growth, reproduction, and maintenance across the life course (DelGiudice, 2018; Geary, 2010; Stearns, 1992). The details of these allocations vary by socioecological context, giving rise to variation in human social behavior that helps inform the sections below. In the face of resource constraints, tradeoffs in life history allocations may appear. Two of the most salient are the tradeoffs between maintenance and reproductive effort and, within reproductive effort, between mating and parenting effort. Variation in testosterone reflects and attunes individual life history allocations. Accordingly, testosterone and related aspects (e.g., androgen receptor variation) of the endocrine system serve as proximate mechanisms that complement ultimate causation (which focuses on how life history allocations influence survival and reproductive success). Life history theory is also concerned with the entire life course. Although the Challenge Hypothesis originally focused on adult male testosterone and social behavior, we also show its relevance prior to reproductive maturation and during reproductive senescence, with those efforts informed by life history theory.

3. Citation analysis of human Challenge Hypothesis research

To situate this human content, we conducted a content analysis of citations of human research drawing upon the Challenge Hypothesis. We chose Google Scholar because it encompasses peer-reviewed articles and books across a breadth of disciplines; this has advantages over more narrowly focused search engines such as PubMed, JSTOR, or PsycInfo. As of December 12, 2018, Wingfield et al. (1990) had been cited 1882 times in Google Scholar. For these 1882 citations, one of us (Gray) coded studies that had humans as a major focus, leaving out reviews or empirical studies focused on other species, or in which humans were peripheral. We relied upon the titles and abstracts available through Google Scholar rather than the actual papers, which means that if details such as study sample size or research design were not reported in these places, then they were not recorded. We evaluated studies published in English. The aim was to provide a portrait of the ways in which the Challenge Hypothesis has shaped human literature. This is not a complete portrait, but one that helps illustrate the bigger picture and sets up the remainder of the present review paper.

We recorded the journal name for peer-reviewed journal publications, publication year, and whether a reference was a review paper or reported original empirical findings. The first discipline affiliation of the corresponding author was recorded to help provide a sense of the interdisciplinary ways in which the Challenge Hypothesis has shaped human literature. Please see Table 1 for further details. Five key behavioral domains were coded: competition (and related concepts of dominance/aggression/status-striving); sexual behavior (and related concepts of courtship/sexuality); partnering (and related concepts of pair-bonding/marriage); parenting (and related concepts of parental care); and other (which encompassed general life history, risk-taking, cognition, among others). These categories were meant to parallel the key behavioral domains (competition, sexual behavior, partnering, parenting) highlighted by the Challenge Hypothesis, and also the structural basis of the present review. When available from the title or abstract, the sample size, sex of research participants, and geographic source of the sample were recorded. Key aspects of the research design were also recorded: cross-sectional vs. longitudinal, experimental (whether manipulating a social variable or testosterone) vs. correlational, and whether testosterone was measured as a part of empirical studies.

Of these relevant Google Scholar search citations of Wingfield et al. (1990), 400 focused on humans. For a single species, this represents a high percentage of these references. By contrast, only a few studies citing the Challenge Hypothesis presented data on chimpanzees or bonobos, our closest living relatives. Information for each variable was not always available, explaining why sample sizes may differ from 400. Of these human-oriented sources, one-third were reviews, the remaining percent with an empirical study focus. These sources were primarily peer-reviewed journal articles. Books or book chapters represented 13.5% of these sources. PhD dissertations represented approximately 10% of sources. PhD Dissertations citing the Challenge Hypothesis have generally appeared in the last decade, and are most frequently awarded by universities in North America and Europe and in the field of Psychology. The most commonly cited journal was “Hormones and Behavior,” followed by “Psychoneuroendocrinology,” “Adaptive Human Behavior and Physiology”, “Evolution and Human Behavior,” and “Physiology and Behavior.” Approximately 85 journals not listed in Table 1 were cited three times or less, illustrating a breadth of interdisciplinary sources.

The first academic affiliation for the corresponding author was Psychology (or an ancillary unit such as Neuroscience) in a slight majority of human-oriented studies. Anthropology was the next most commonly represented academic affiliation. A scattering of other disciplinary backgrounds including Medicine, Biology, and Business also appeared, providing a sense of the interdisciplinary breadth of this human scholarship. It might be noted that if additional author

Table 1
Descriptive data for Google Scholar content analysis.

Measure	N	%
Type of research source		
Original empirical research	267	66.8
Review	133	33.3
Most commonly cited (journal) sources		
Books/book chapters (all combined)	54	13.5
Hormones and Behavior	51	12.8
Psychoneuroendocrinology	20	5.0
Adaptive Human Behavior and Physiology	17	4.3
Evolution and Human Behavior	14	3.5
Physiology and Behavior	13	3.3
American Journal of Human Biology	9	2.3
Proceedings of the Royal Society of London B: Bio Sciences	8	2.0
Archives of Sexual Behavior	8	2.0
PLoS ONE	7	1.8
Proceedings of the National Academy of Sciences	6	1.5
Human Nature	6	1.5
American Journal of Physical Anthropology	4	1.0
Biological Psychiatry	4	1.0
Neuroscience and Biobehavioral Reviews	4	1.0
Behavioral phenotypes		
Competition/aggression/status	189	48.2
Sexual behavior/courtship/sexuality	29	7.4
Partnering/pair-bonding/marriage/relationship dynamics	43	11.0
Parental status/parental care	54	13.8
Other (e.g., risk-taking, gender differences, life history theory)	77	19.6
First academic affiliation of corresponding author		
Psychology/brain sciences/cognitive science	190	56.9
Anthropology	50	15.0
Medicine/public health	20	6.0
Business/marketing	17	5.1
Biology	10	3.0
Other	9	2.7
Sociology	8	2.4
Exercise physiology/sports science	6	1.8
Family and human development	6	1.8
Communications	5	1.5
Government/political science	5	1.5
Economics	4	1.2
Education	3	0.9
Research subjects		
Males only	103	52.2
Females only	24	12.2
Both males and females	70	35.5
Sample size		
≤24	17	10.5
25–≤49	24	14.8
50–≤74	20	12.3
75–≤99	21	13.0
100–199	39	24.1
200–499	24	14.8
500–999	9	5.6
≥1000	8	4.9
Testosterone measured or given in original research studies		
Yes	201	81.4
No	46	18.6

affiliations were included or even a given author's affiliation over time (e.g., a postdoc in Business or Medicine prior to a faculty position in Psychology or Anthropology) then more evidence of interdisciplinary integration would emerge. If considering the national base of academic affiliations, most were in North America or Europe. Relatively few if any corresponding authors were from China, India, Brazil, Russia or other countries outside the Cultural West, showing the current limits of scholarly leadership inspired by the Challenge Hypothesis. If non-English sources were included, a small but wider geographic background among corresponding authors would have emerged, with a sense that scholars in recent years from Mexico, Brazil and China are at the early stages of conducting research framed by the Challenge Hypothesis.

The vast majority—88%—of studies had male subjects, and approximately one-third of studies included males and females. The Challenge Hypothesis was formulated on male avian research, with this emphasis apparent in the human literature, though also with a notable fraction of studies involving females or even exclusive focus on females. Half of sample sizes were fewer than 100 individuals. At the smallest end of that spectrum, some studies conducted among elite athletes had sample sizes under 25. By contrast, larger samples often drew upon university-based or community-based samples in correlational designs. In the vast majority—81%—of original, empirical research studies, testosterone was either measured (e.g., in saliva or blood) or administered. In a few of the studies with large sample sizes, testosterone was not measured but the Challenge Hypothesis was cited for its conceptual relevance (e.g., male-male competition). The sample sizes of empirical studies in which testosterone was measured tended to be relatively high compared to nonhuman literatures, one of the benefits of working with an abundant and globally-distributed species. Anthropologists appeared more likely to report on non-European-based samples, illustrating greater concern with human cross-cultural diversity and helping obviate bias concerns over Western, Educated, Industrialized, Rich, and Democratic (WEIRD) samples (Henrich et al., 2010). Outside of North America and Western Europe, sources explicitly referenced samples drawn from Cebu City, Philippines (at seven citations, the most for any such location); Singapore; China; Bangladesh; The Gambia; Senegal; Republic of the Congo; Kenya; Tanzania; Dominica; Jamaica; rural Bolivia; rural Ecuador; and Brazil. The majority of scholars did not note the geographic source of the sample in the Abstract, perhaps because that was not deemed a central explicit element in research design. It may often be inferred, particularly for studies led by psychologists, that subjects were undergraduate students at a university. Under that view, the vast amount of research involved North American and European subjects, primarily undergraduate students and, to a lesser degree, community-based samples.

The majority of original, empirical studies were correlational and could be divided in two categories: those testing correlations between demographic (e.g., paternal status) or questionnaire-based measures and testosterone levels, and those testing testosterone responses to a social context, such as a competitive athletic encounter or an interaction with a child. A handful of studies involved longitudinal designs. These included a birth cohort study in Cebu City, Philippines (Gettler et al., 2011), and several studies involving multiple sampling across pregnancy or childbirth in Western samples (Edelstein et al., 2011; Perini et al., 2012a). In more recent years, experimental evaluations of effects of one-time exogenous testosterone administration (18 such empirical studies in this sample) have been undertaken to determine effects on outcomes such as responses to angry faces (for a recent review, see Zilioli and Bird, 2017). In other studies, experimental manipulation of a social variable (particularly winning or losing in a lab-based competition) was undertaken to determine effects on testosterone. A few studies involved brain imaging to evaluate neural responses in concert with testosterone responses to competitive, sexual, and parental stimuli. Apart from testosterone, cortisol is the other most commonly measured hormone in this sample. Other hormones, such as dehydroepiandrosterone (DHEA), androstenedione, oxytocin, and prolactin were occasionally measured as well.

Fig. 1 depicts the number of human studies citing Wingfield et al. (1990) across time with respect to key behavioral domains. For studies featuring multiple behavioral domains, the most central one from each study was identified. As these patterns reveal, the most commonly cited domain is competition/aggression, appearing in 48% of studies. The other behavioral domains comprise 7–20% of studies each. The first study focused on partnering was published in 2002 (Gray et al., 2002), and the first on parenting in 2000 (Storey et al., 2000). The overarching patterns point to increasing rates of publications from 1990 until recently. Although not depicted in this Figure, the studies with non-European samples citing the Challenge Hypothesis tend to focus on partnering and parenting rather than competition/aggression or sexuality/courtship.

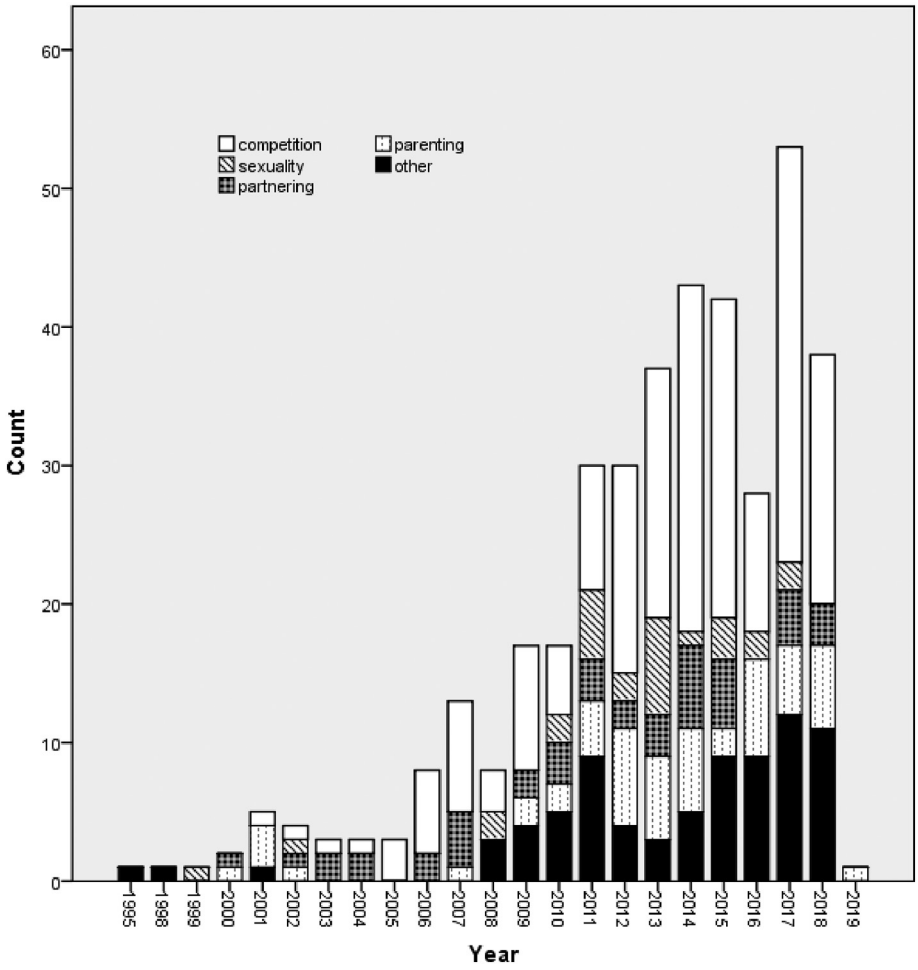

Fig. 1. Frequency data for primary behavioral domains of human empirical studies.

4. Testosterone and competition

Given the original focus of the Challenge Hypothesis on avian testosterone, mating, and intrasexual competition, it is perhaps unsurprising that a considerable portion of the human literature has also been dedicated to understanding the relationship between testosterone and competition. A full review is beyond the scope of the present paper, but recent reviews and meta-analyses (Carre and Olmstead, 2015; Casto and Edwards, 2016; Geniole et al., 2017; Zilioli and Bird, 2017), in addition to other contributions in the current special issue (*insert citations when available) provide additional details on this topic. Nevertheless, we provide a brief overview here of some of the major trends and findings in this area, as they have considerably advanced our understanding of how the Challenge Hypothesis and the related life-history framework apply to humans.

The Challenge Hypothesis posits that among males, testosterone concentrations reach their peak during intrasexual (i.e., male-to-male) competitive interactions, and that these changes facilitate territorial or aggressive behavior. In support of this, research in humans has found that testosterone fluctuates rapidly in response to competitive contexts, including both athletic (Cook and Crewther, 2012b; Gaviglio et al., 2015; Salvador et al., 2003) and non-athletic competitions (Carre et al., 2009; Casto and Edwards, 2016; Mazur et al., 1992). Further, research also indicates that transient changes in testosterone predict future behavior, consistent with the Challenge Hypothesis (Carre et al., 2009; Zilioli and Bird, 2017). For example, a rise in testosterone following competition predicts willingness to compete again (Carré et al., 2008), increased aggressive behavior (Carré and McCormick, 2008), athletic performance and physical strength (Cook and Crewther, 2012a, 2012b), and better performance on the same competitive task the next day (Zilioli and Watson, 2014). Thus, consistent with a broader application of the Challenge Hypothesis, existing evidence suggests that among humans, testosterone changes rapidly in the context of same-sex competition, and such changes modulate ongoing behavior in the same domain.

5. Winners and losers

Some of the work on testosterone and competition has placed a focus on how the outcome of the competition (i.e., win or loss) might modulate testosterone reactivity and future behavior. The Biosocial Model of Status (Mazur and Booth, 1998; Mazur and Michalek, 1998; Mazur, 1985) is conceptually similar to the Challenge Hypothesis, with the additional prediction that testosterone will increase in winners and decrease in losers. Theoretically, this model suggests that winners of competitive encounters potentially face additional challenges for social status, and therefore a transient increase in testosterone helps to promote behavior (e.g., aggression, future competition) that can serve to defend or further promote one's status. Among losers, a decrease in testosterone could serve to promote retreat or other behavior geared toward further status loss.

A recent meta-analysis examining competition-testosterone research over the last three and a half decades found results in line with the ideas proposed by the Challenge Hypothesis and the Biosocial Model of Status, showing that on average, winners of competitions show a larger increase in testosterone relative to losers for both men and women

(Geniole et al., 2017). Effects from this analysis were heterogeneous, however, finding that studies conducted outside the confines of a laboratory showed larger effects than controlled laboratory competitions, and that such effects were specific to men. As two of several possible explanations for the findings, the authors speculated that a) competition may be more salient and come with more investment in more natural settings like sports competitions versus the confines of a laboratory, and b) events outside of the laboratory often involve spectators, which may influence the strength of any "winner-loser" effects. As potential support for this, Miller et al. (2012) found that the ratio of men to women spectators influenced the strength of the winner-loser effect in a Frisbee competition.

Some work has also found that testosterone increases are larger when a team wins in their home venue relative to winning in the opponent's venue (Carré, 2009). Others showed that the effects of testosterone from competition (or from exogenous administration) on social perception, cognition, decision-making, and behaviors relevant to status (e.g., aggression, preference for status goods) may depend critically on motivational variables such as trait dominance (Bird et al., 2017, 2019; Carre et al., 2017; Carré et al., 2008; Geniole et al., in press) and self-construal (Welker et al., 2017), as well as physiological variables like prenatal exposure to testosterone (Auyeung et al., 2009), basal cortisol (Mehta and Josephs, 2010), and basal testosterone (Welling et al., 2016). Collectively, this growing literature adds nuance to the application of the Challenge Hypothesis to humans. These findings suggest that in competitive contexts where mating cues (e.g., number of women at a sporting event) or territoriality (e.g., home versus away) are more salient, or when motivational (e.g., trait dominance) or physiological variables (e.g., 2D:4D ratio) increase sensitivity to testosterone change or orient an individual more toward status-relevant behaviors (e.g., personality), testosterone may either respond more strongly to competitive outcomes, or may show a stronger link with future behavior, presumably as a way to help calibrate ongoing status-related concerns. Future work will help clarify such situational, motivational, and physiological modulation of the effects of competition on testosterone change, and testosterone change on future behavior (Bird and Zilioli, 2017; Zilioli and Bird, 2017). Additional work can expand the individual and coalitionary contexts in which testosterone and other hormone responses to competition are evaluated, such as a growing esports (video game playing) industry (Gray et al., 2018).

6. Testosterone responses to mating-relevant stimuli and courtship

Wingfield et al.'s (1990) work in avian species revealed that testosterone reached a physiological maximum in response to competitive interactions, and this increase in testosterone functioned to help facilitate aggressive and territorial behavior. A body of research in humans showed that in addition to changing rapidly after competitive encounters (Carre and Olmstead, 2015; Geniole et al., 2017), testosterone also fluctuated rapidly in response to mating-relevant stimuli (Gray et al., 2017a; Roney and Gettler, 2015; Zilioli and Bird, 2017). From a functional perspective, these testosterone fluctuations have been hypothesized to fine-tune behaviors relevant to reproductive success. Some research indirectly supports this idea. For instance, Flinn et al. (2012) found that among a small sample of men in a rural Dominican community, interacting with potential mates predicted an increase in testosterone relative to interactions with conjugal partners of close friends or with female kin. Other work found that young male skateboarders performing in front of an attractive female (vs. a male) took more risks in trying to land harder tricks, and that this association was associated with higher levels of testosterone. The authors interpreted this finding as evidence that testosterone could function to increase sexual display strategies (Ronay and Hippel, 2010). Complementary work showed that sexual thoughts were themselves not enough to potentiate the release of testosterone (Goldey and van Anders, 2012), possibly because a mating opportunity was not salient, and thus the potential costs associated with testosterone release (e.g., immunosuppression; see Goldey and van Anders, 2015, for a review) were avoided.

Although work on the functional significance of acute testosterone changes is still in the early stages, a more established literature has examined how exposure to mating-relevant stimuli affects testosterone release. In the following sections, we first review some of the literature on testosterone responses to mating-relevant stimuli and courtship. Next, we discuss how the stimuli-testosterone and testosterone-behavior relationships may be modulated by context, personality variables and other factors. We further discuss the idea that changes in testosterone might be modulated by the degree of perceived threat to a mating opportunity—an area that has received less attention in the literature and that may be a suitable avenue for future investigations.

7. Testosterone responses to mating-relevant stimuli

In male rats, luteinizing hormone (LH) increased in response to female-related stimuli (Coquelin and Bronson, 1980), including the mere sight of a female conspecific (Katongole et al., 1971) and female urinary pheromones (Clancy et al., 1988; Richardson et al., 2004). Further, in males of a variety of mammalian taxa—including not only rats (Bonilla-Jaime et al., 2006; Macrides et al., 1975), but also other species such as sheep (Borg et al., 1992) and monkeys (Cerda-Molina et al., 2006; Ziegler et al., 2005)—exposure to female conspecifics resulted in elevated testosterone. These elevations were particularly pronounced during the initial exposure to a female, even in the absence of physical interactions with her (Amstislavskaya and Popova, 2004), and following ejaculation (Coquelin and Desjardins, 1982; Nyby, 2008). Interestingly, although being sexually experienced leads to a more robust androgenic response, it is not a requirement for these responses (Clancy et al., 1988). Notably, this hormonal reflex is modulated by mating system and mating status (Ziegler et al., 2005), novelty of the female stimulus (Coquelin and Bronson, 1980), and social status (Surbeck et al., 2012).

Work in humans also supports the hypothesis that exposure to mating-relevant stimuli is associated with an increase in testosterone. In some of the earliest work, Roney et al. (2003) found that when college-aged men were assigned to have a short conversation either with a woman or with a man, those speaking with a woman showed a significant increase in testosterone relative to baseline—an association that was not found for those assigned to speak with a man. In two follow-up experiments, Roney et al. (2007) found that conversing with a woman predicted increases in testosterone relative to waiting alone in a room, and, in the second experiment, that men interacting with a flirtatious female confederate (vs. men interacting with a friendly male confederate) experienced significant elevations in testosterone. Following Roney et al.'s seminal work (2007), other investigations have supported the notion that testosterone increases rapidly in response to mating-relevant stimuli. For example, Zilioli et al. (2014) found that when exposing male and female participants to photographs of men's and women's faces, extended viewing of opposite sex photos, but not same sex photos, predicted an increase in testosterone. Other work found that exposing men to periovulatory axillary (armpit) and vulvar odors increased men's testosterone and cortisol, with the most prolonged effect (i.e., at later post exposure measurement points) for vulvar odors (Cerda-Molina et al., 2006). Interestingly, the same odors also predicted an increased interest in sex, as measured by a self-report questionnaire administered after exposure to the odors (Cerda-Molina et al., 2013). Conceptually similar work found that exposing men to t-shirts of ovulating women predicted increased testosterone responses relative to t-shirts of non-ovulating women and unworn t-shirts (Miller and Maner, 2010; but see Roney and Simmons, 2012).

As in the case of testosterone fluctuations in response to male-to-male competitive interactions, context seems to qualify testosterone

responses to mating-relevant stimuli (Zilioli and Bird, 2017). For example, Miller et al. (2012) found that ratios of opposite- to same-sex individuals at a sporting competition—signalling potential competition over mating opportunities—were positively correlated with testosterone release among competitors. Other work has found that men's testosterone increases at a sex club, and the highest increases in testosterone were found among men directly participating in sexual activity (vs those watching)—further suggesting sensitivity of testosterone release to potential mating opportunities and competition with other men (Escasa et al., 2011). Similar to work showing that testosterone release as a result of mating opportunities predicts potential sexual displays (Ronay and Hippel, 2010), another investigation found that men with elevated testosterone following a competition showed more affiliative behaviors in informal interactions with women than with men (e.g., smiled more, showed more interest, made more eye contact) (van der Meij et al., 2011). Taken together, the current literature provides some support for the Challenge Hypothesis as applied to humans, where exposure to mating-relevant stimuli predicts testosterone release, with modulation by salience of, and competition over, mating opportunities.

8. The role of personality traits and other individual factors

In addition to context, individual differences have also been found to modulate testosterone reactivity to mating-relevant stimuli. van der Meij et al. (2008) found that male participants informally conversing with another man showed a non-significant drop in testosterone, while male participants informally conversing with a woman showed a significant rise in testosterone. Notably, this effect was stronger among men with dominant, aggressive personality traits—perhaps because these men seek more short-term mating opportunities (van der Meij et al., 2008). Interest in short-term relationships, as opposed to long-term ones, may itself modulate testosterone responses to sexual stimuli. Using men's interest in babies as a proxy for long-term mating interest, Zilioli et al. (2016) showed that men who reported low interest in babies (i.e., an indicator of short-term mating orientation) responded to an erotic video with larger increases in testosterone than did men with high interest in babies.

Other work has found that biological variables that influence the action of testosterone also moderate testosterone responses to mating-relevant stimuli. For instance, Roney et al. (2010) examined the extent to which cortisol, and the length of men's CAG repeats in the androgen receptor gene—the number of CAG repeats being inversely related to androgen sensitivity (Chamberlain et al., 1994)—moderated men's testosterone reactivity to interactions with women. Results not only revealed that testosterone rose significantly following interactions with women (but not men), corroborating previous findings (Roney et al., 2007), but also that such increases were the strongest among men with low CAG repeats (high androgen sensitivity) and low cortisol.

Lastly, exogenous administration studies have helped shed some light on the causal link between testosterone release and mating behavior. For example, Bird et al. (2016) found that men given a single dose of testosterone (vs. placebo) showed stronger preferences for women's faces that were more characteristically feminine. This effect was, however, seen only when the men were indicating preference for a short-term partner rather than a long-term partner. Recent work on exogenous testosterone also supports the idea that the influence of testosterone on behaviors relevant to reproductive success, such as aggression (Carre et al., 2017; Geniole et al., in press), cooperation (Bird et al., 2019), and competitive decision-making (Mehta et al., 2015), are moderated by an individual's self-construal, dominance, and impulsivity. For example, Carre et al. (2017) found that a single dose of testosterone rapidly increased aggressive behavior on a laboratory task, but only among men who were high in trait dominance or impulsivity. Replicating and extending this finding, Geniole et al. (in press) found that testosterone increased aggressive behavior, but only among men with high androgenic sensitivity (low CAG repeats) and who were high in a personality "risk factor" that indicates high dominance, high impulsivity, and highly independent self-construal, the latter indicating a tendency to see one's self as relatively independent (rather than interconnected) with others. Thus, the degree to which testosterone exerts its effects on mating-relevant behaviors may depend on personality traits and other factors, just as testosterone reactivity following exposure to various stimuli may also depend on these factors.

9. Testosterone and threats to courtship

One idea stemming from the Challenge Hypothesis that has not received much attention in the literature is the possibility that changes in testosterone might be modulated by perceived threat to a mating opportunity, as opposed to general competitive encounters not directly related to mating (e.g., sports, chance-based tasks like a coin toss; Parmigiani et al., 2006; McCaul et al., 1992). Fales and colleagues' and Goetz et al.'s work provides some insight on this topic. Fales et al. (2014) randomly assigned men in heterosexual relationships to view photos and profile descriptions of ten highly-competitive male rivals—as defined by observer-rated attractiveness and self-reported competitive nature—or ten low-competitive male rivals during periods of high or low fertility of their romantic partner's cycle. To increase the salience of rivalry, participants were told that the men in the photos attended the same school as them and that their own romantic partner would be rating the same men's faces for physical attractiveness. Consistent with the prediction that testosterone dynamics are sensitive to courtship threats, the authors found that men exposed to the high-competitive rivals showed significantly higher testosterone after the task on fertile days—a time with increased conception risk from an intrasexual rival—relative to non-fertile days of their partners' cycle.

In addition to men showing greater testosterone reactivity to perceived mating threat, other work suggests that testosterone reactivity may then lead to increased activation in threat-related brain areas, perhaps serving to facilitate action aimed at minimizing or eliminating such threat. In their study, Goetz et al. (2014) first administered a gonadotropin releasing hormone (GnRH) antagonist to participants in order to bring their testosterone levels to a common baseline. The GnRH manipulation was then followed by the administration of testosterone or placebo in a within-subjects, cross-over design. Following hormone administration, participants were placed in a brain scanner to complete a face-rating task where they were exposed to different facial expressions, including those showing anger—an expression typically associated with threat. Results revealed that the administration of testosterone relative to placebo predicted heightened reactivity of the amygdala, hypothalamus, and periaqueductal grey in response to angry facial expressions. While this study did not examine courtship threats directly, it provided indirect evidence to suggest that an increase in testosterone may increase perceptions of threat more generally, which in turn may facilitate behavior aimed at the reduction or elimination of such threat. If such findings generalize to threats to courtship, it serves to reason that a transient increase in testosterone could upregulate threat-related brain function, in turn promoting behavior that would prevent a loss of mating opportunities.

The possibility that testosterone release is strongest in the face of threats to courtship (vs. general competitive encounters), and that such changes in testosterone facilitate ongoing behavior in the mating domain (e.g., mate guarding), will require direct tests in future work. Findings will likely be strengthened by both exogenous administration to establish causal effects of transient increases in testosterone on relevant behavior, and examining endogenous fluctuations in hormones following exposure to a courtship threat (e.g., another individual flirting with one's romantic partner).

10. Reduced testosterone, mating effort, and parenting effort

Wingfield et al.'s (1990) seminal work in avian species provided an important clue into the dynamic relationship between testosterone, mating, and paternal care in humans. In addition to reviewing findings that testosterone levels rose at the beginning of the breeding season and subsequently reached a physiological maximum in response to intrasexual encounters, it was also discovered that the expression of paternal care required a temporary *decrease* in testosterone secretion. This patterning provided important evidence to suggest that testosterone plays a role in mediating some of the behavioral processes involved in life history trade-offs (Grebe et al., 2019; Gray et al., 2017a; Hau and Wingfield, 2011; Zilioli and Bird, 2017). In this case, testosterone is proposed to mediate the trade-off between mating and parenting effort.

Inspired by Wingfield's work, research in humans has provided considerable evidence to suggest that testosterone is generally lower in contexts with reduced mating effort and/or greater parenting effort. For instance, in a longitudinal examination of the extent to which partnering, fatherhood, and paternal caregiving were prospectively associated with testosterone levels, Gettler et al. (2011) found that the greatest decreases in testosterone over a 5-year study were for men who married and had a child (relative to those who remained single and childless over the study). Further, examination of childcare investment showed that fathers providing the most care to young infants had the lowest levels of testosterone. Such findings have helped bolster correlational evidence showing that men in committed, romantic relationships had lower testosterone relative to single men (reviewed in Gray and Campbell, 2009 and Grebe et al., 2019; see also Gray et al., 2017a), and that men with lower testosterone showed higher scores on indices of parental investment (Mascaro et al., 2013), and relationship quality (Das and Sawin, 2016; Gray et al., 2017b).

Some work shows important contextual variation in the relationship between men's testosterone and paternal behavior, revealing potential modulation by variables such as the degree of parental involvement that is typical of a population. For example, Muller et al. (2009) found that among the Hadza in Tanzania, a group with typically high levels of paternal involvement, testosterone levels were lower for men who were engaged in parental care. In contrast, however, the authors found that among the Datoga, a population typically exhibiting low levels of parental involvement, fathers had similar levels of testosterone to those of non-fathers. A separate study (Alvergne et al., 2009) found that among a largely polygynous population of agriculturalists in Senegal, investment in parental care predicted testosterone levels such that highly investing fathers had the lowest morning testosterone. Further, among men under 50 in this study, polygynous men had higher testosterone levels than monogamous men, similar to findings in Kenyan Swahili men showing that polygynously married men with two wives had higher testosterone than men with no wife or one wife only (Gray, 2003).

More nuanced findings have also emerged, such as work by Muller et al. (2009) showing not only the inverse relationship between general offspring care and testosterone levels, but also the importance of considering the age of the child; indeed, the authors found that fathers caring for younger children—who require more time and attention—showed a larger decrease in testosterone over the day than fathers with older children. Such findings are conceptually similar to those showing that men with younger biological children also tend to have lower levels of testosterone (Gray, 2003). In other work, Perini et al. (2012a) found a significant decrease in relationship tenderness (positive caring or appreciative behaviors) and togetherness/communication (feelings of closeness and tendency to communicate about events) in fathers relative to fatherless controls, but also found that changes in relationship quality were strongest among fathers with the largest change in testosterone levels over time. A separate analysis of the same dataset also found that sensation-seeking interacted with testosterone such that at the end of the study, fathers with low sensation seeking—a personality trait typically associated with mating behavior and elevated testosterone—also showed the lowest testosterone (Perini et al., 2012b).

One pattern that emerges from the human literature on male testosterone, partnering, and parenting is the behavioral plasticity, which also resonates with the Challenge Hypothesis's recognition that social context is crucial to situating changes in reproductively-aged male testosterone. The Challenge Hypothesis conceptualized patterns of male testosterone in light of initial partnering, re-partnering, mating polygynously, and paternal care. Humans exhibit considerable cross-cultural and historic variation in partnership and paternal dynamics (Gray and Garcia, 2013; Low, 2015; Marlowe, 2000a), effectively providing an array of natural experiments on variation in mating and parenting effort. Pertinent to the Challenge Hypothesis, four studies have investigated the relationship between male testosterone and polygynous marriage, with several of those cited above. In the most recent such study, among farmers in rural Gambia, men with multiple wives had higher testosterone levels than monogamously married men (Lawson et al., 2017). This study also pointed to complex shifts in male mating and parenting effort with advancing age, a topic we will discuss further below. In the Gambian sample, men were more likely to be married as they grew older, thus heavily confounding age and marital status, even as monogamously married men had lower testosterone than single men.

The Challenge Hypothesis did not comment on sexual orientation or same-sex reproductive behavior, with the framework implicitly focused on heterosexual behavior. However, same-sex sexual behavior in non-human animals is widely recognized and can also include same-sex partnerships (e.g., same-sex avian partners that might incubate eggs or rear chicks together) (Poiani, 2010). Several human studies investigated correlations between adult testosterone, partnership status, and parental status. In the first such study, van Anders and Watson (2006) found that men and women partnered with women (which thus included same-sex partnered women and heterosexual men) had lower testosterone than singles or women and men partnered to men. Put another way, partnered gay men did not differ in testosterone compared with single gay men, whereas lesbians in partnerships did have lower testosterone than single lesbians. However, in a different Canadian sample, sexual orientation did not differentially predict women's testosterone across relationship status, with partnered women (regardless of sexual orientation) having lower testosterone than single women (van Anders and Watson, 2007). In a study of 48 gay couples, gay partnered fathers did not have different testosterone levels than gay partnered non-fathers (Burke and Bribiescas, 2018).

Other important variables, such as personality and sexual proclivity, have also been shown to modulate the relationship between mating/parenting effort and testosterone levels. For instance, some work has found that sociosexual orientation may function as a proxy of mating effort, as partnered men with an openness to uncommitted sex (i.e., an “unrestricted” sociosexual orientation) showed testosterone profiles similar to those of single men (Edelstein et al., 2011). Similarly, McIntyre et al. (2006) found that romantic involvement predictably reduced men's testosterone levels, but not among men who maintained a high level of extra-pair sexual interest. In a longitudinal investigation, new fathers were shown to have significant declines in testosterone, and those with the largest drops reported less frequent sex; however, among those new fathers who maintained high sexual activity over the course of the study (4.5 years), declines were not as drastic (Gettler et al., 2013). Thus, pair-bonding appears associated with a decrease in testosterone—as would be expected by the Challenge Hypothesis in the context of reduced mating—but this same relationship is not evident for men who do not actually show measures of reduced mating effort as indexed by higher levels of sexual interest and activity.

Research has also investigated how transient changes in testosterone vary in contexts where partnering and/or parenting is salient. The Challenge Hypothesis predicts that overall parenting behavior would generally be associated with a decline in testosterone, but some

work suggests important moderators of such effects (reviewed in Zilioli and Bird, 2017). For example, van Anders et al. (2012) examined the extent to which men's testosterone reactivity varied as a function of hearing baby cries and also opportunities to provide nurturance to a realistic baby doll. The authors found that in response to hearing the baby cries, men's testosterone decreased, but only if they were able to successfully comfort the crying doll via nurturant behavior. For men who were not able to comfort the doll (as determined by experimental manipulation of the doll settings), testosterone levels were similar to those of men in the control condition (where participants simply flipped through a book containing scenic photography to control for exposure to stimuli and the passing of time). In contrast to all other conditions, for men who heard baby cries but could not interact with a baby, testosterone actually increased. The authors concluded that with respect to parenting, only nurturant behaviors are related to low testosterone, while those that might elicit some form of challenge or threat (such as a crying baby without opportunity to comfort) would be linked to higher testosterone. This finding constitutes a key idea of the Steroid-Peptide Theory of Social Bonds (van Anders et al., 2011), an extension of the Challenge Hypothesis framework suggesting that in parenting contexts that invoke a protective or defensive response, testosterone will increase, whereas those invoking nurturant behavior will predict a testosterone decrease.

Research on transient changes in male testosterone with respect to putative parenting effort has included naturalistic studies that complement the more controlled lab research just highlighted. With a focus on Tsimane forager-horticulturalist men in lowland Bolivia, transient increases in men's testosterone while engaging in farming (tree-chopping) and hunting activities were interpreted as physiological responses to indirect parenting effort, namely provisioning (Trumble et al., 2013, 2014). Among a small sample ($n = 16$) of fisher-farmer fathers in the Republic of Congo, men with intermediate testosterone were ranked as the best providers and their children scored highest on health measures (Boyette et al., 2019). While older men and partnered fathers had lower testosterone than single non-fathers in a rural Polish sample of farmers, age-related declines in men's testosterone were not related to muscle or strength, suggesting that men's testosterone was not directly tied to physiological support for physical provisioning (Alvarado et al., 2015). The Challenge Hypothesis did not categorize parental care into what are frequently viewed as different forms of investment that may be differentially linked to testosterone: protection, provisioning, direct childcare, and social transmission (Gray and Crittenden, 2014).

The degree to which testosterone levels play a causal role in later partnering or parenting, or whether partnering or parenting causes changes in testosterone, remains an open question. Some work is more consistent with a “trait” perspective, suggesting that men with lower testosterone may be more inclined to enter and remain in partnerships (Gray et al., 2004). This is also consistent with the high intra-subject correlations across sample collection in men's testosterone (Dabbs and Dabbs, 2000). In contrast, other work is consistent with a “state” perspective, suggesting that partnering status affects testosterone levels (e.g., Gettler et al., 2011). Recently, a longitudinal study found both evidence for trait associations, as well as preliminary evidence to suggest the possibility of bidirectional associations. In a sample of 78 undergraduate men, the authors found not only that testosterone predicted future partnering status, but also that testosterone responded to changes in relationship status, where relationship dissolution increased men's testosterone (Dibble et al., 2017). In a longitudinal study of over 1100 Danish men 30–60 years of age, shifting from singlehood to marriage was associated with a more pronounced decrease in testosterone across time than remaining single or married, whereas divorcing led to an attenuated age-related decrease in testosterone (Holmboe et al., 2017). It remains possible that other variables such as sleep, body composition, male age and health status could contribute to changes in testosterone and behavior; given that many studies control for these most obvious covariates, they are unlikely to fully account for the patterns in male testosterone and family variables reported above. Future work is needed to determine the causal role that testosterone and/or partnering play in shifting behavior and hormones, specifically, and how findings fit within the framework originally set out by the Challenge Hypothesis.

One way to establish causal pathways is via pharmacological manipulation of testosterone (for overview of administration studies, see Zilioli and Bird, 2017; see also Bos et al., 2012). To date, there are no existing studies testing the causal role of testosterone on intimate partnership or paternal behavior. Existing paradigms may provide a useful means to test hypothesized directions of effects in these domains. For example, to test whether testosterone plays a causal role in suppressing paternal behavior and/or increasing mating behavior, fathers could be assigned to receive testosterone or placebo, and then be given an opportunity to interact with their baby or a baby doll to measure their engagement in nurturant behavior (Zilioli and Bird, 2017). Further information could be gathered by including an opposite sex confederate. If testosterone plays a causal role in suppressing nurturant behavior and/or increasing mating effort, it might be expected that men on testosterone, relative to men on placebo, would show less time with the child or doll and more time talking with the opposite sex confederate.

Beyond single administration studies, men receiving testosterone replacement therapy (TRT) may provide a useful population for testing various hypotheses. It is possible that men transitioning to TRT would see a concomitant increase in mating effort and a decrease in parental care as predicted by the Challenge Hypothesis (Archer, 2006; Zilioli and Bird, 2017). However, TRT on average is prescribed to men in later stages of life at a time when testosterone levels are lower (Allan and McLachlan, 2004; Rao et al., 2017) and when mating concerns are arguably less salient. Examination of the effects of TRT on mating and paternal behavior, stratified by age groups, may reveal useful data for testing hypotheses about these potential effects. For example, it might be expected that among younger men, TRT will increase interest and/or effort in mating and decrease interest and/or effort in paternal care. In older men, however, it is possible that TRT has a positive impact on other variables, such as those contributing to well-being (e.g., mood; Wu et al., 2010), which in turn may foster more involvement with family, rather than a greater interest in mating.

As with other behaviors such as athletic competition, it remains unclear whether theory would anticipate, or empirical data support, testosterone having a similar role in women as it does in men. The recognition that a hormone can be selected for functions in one sex, yet exert similar effects on the other sex (Ketterson and Sandell, 2005), offers inspiration to think testosterone may be similarly related to women's reproductive behaviors as it is to men's. Effects of exogenous testosterone administration (Wierman et al., 2014) or of clinical conditions such as polycystic ovary syndrome (PCOS) (Manlove et al., 2008), characterized by elevated androgens, can help reveal whether testosterone in women has effects consistent with the Challenge Hypothesis. Correlational research on women recruited from community samples can also enable testing whether, like in men, partnering or parenting status predict women's testosterone. In samples of women in Norway (Barrett et al., 2013) and Cebu City, Philippines (Kuzawa et al., 2010a), mothers had lower testosterone levels than similarly aged non-mothers. However, comparative non-human evidence and human observational studies suggest that estrogen likely has a more powerful link to human female sexual desire and mating effort than testosterone (Cappelletti and Wallen, 2016).

Other work from a large representative study of US men and women focused on testosterone and depression found that for fathers, higher testosterone was associated with lower prevalence of mild depressive symptoms, but this was specific to fathers who were high in socioeconomic status; in contrast, fathers with high testosterone but *low* socioeconomic status had modestly elevated depression risks (Gettler and Oka, 2016). Thus, the relationship between testosterone, nurturant

behavior, and mating effort in older men may be more complex than the traditional framework of the Challenge Hypothesis. Future work directly testing hypotheses about the pathways through which testosterone might influence nurturing or mating behavior (e.g., mood, energy), in addition to potential socioecological moderators (including those highly relevant to status, such as socioeconomic status), will help shed further light on this topic.

11. Life history extensions of the challenge hypothesis: perinatal and juvenile development

The Challenge Hypothesis has traditionally been applied to the interpretation of testosterone fluctuations in adult males of prime reproductive ages, consistent with the idea that testosterone facilitates intrasexual competition when mating is most salient (Archer, 2006; Geniole et al., 2017; Mazur and Booth, 1998; Oliveira and Oliveira, 2014; Wingfield et al., 2018). This does not preclude the possibility that the theoretical implications of the Challenge Hypothesis may be used to model factors that shape steroid hormone responses during social challenges and manifestations of aggression at earlier (e.g., childhood) or later (see: senescence section) human life history stages, however. In this section, we briefly discuss the relationship between perinatal organizational effects of androgens as developmental contributors to behavioral plasticity, and a small set of findings suggesting that steroid hormones other than testosterone may be involved in human juvenile responses to competitive challenges. We also discuss key contributions from the nonhuman animal literature that provide complementary support for the role of adrenal androgens in the context of juvenile competition and aggression.

A recognition that the testes are active during gestation and early infancy raise the question of whether early testosterone exposure during perinatal development influences developmental plasticity in male life histories. Plasticity, in this context, refers to the capacity of an organism to generate variable phenotypes in response to stressors (e.g., environmental and psychosocial) and variable levels of androgen exposure in utero and during early infancy. For boys, the first few months of life are characterized by transient activation of the hypothalamic-pituitary-gonadal axis (i.e., mini-puberty). Between 3 and 6 months of age, boys produce a surge of testosterone that is linked to long-term organizational effects on psychosexual behavior and development (e.g., higher testosterone levels were associated with early sexual maturation, higher numbers of lifetime sexual partners, and sex-typed play behaviors) (Kuzawa et al., 2010a, 2010b; Lamminmaki et al., 2012). Additional studies on prenatal and postnatal testosterone levels have further identified downstream effects of early testosterone exposure on rates of aggression, risk-taking, increased muscularity, and accelerated sexual development, traits which are intrinsically associated with the Challenge Hypothesis and lifetime reproductive success in males (Kuzawa et al., 2010a, 2010b; Martel, 2013). High early testosterone exposure has also been shown to influence reproductive strategies, male sex-typed play interests among pre-school children, sexual differentiation, and amplification of plasticity to environmental factors (e.g., prenatal stress, early infections, social stressors in childhood) (Auyeung et al., 2009; Berenbaum and Beltz, 2011; Del Giudice et al., 2018; Lamminmaki et al., 2012). These data support the view that early life stressors and testosterone exposure are likely important factors influencing male life history strategies.

The extent to which testosterone or adrenal androgens are related to, and potentially promote, competitive and aggressive behavior during middle childhood remains less clear, with much of that earlier work focusing on young pubertal or post-pubertal boys utilizing correlational analyses (Azurmendi et al., 2006; Azurmendi et al., 2016; Golubchik et al., 2009; Ramirez, 2003). Several studies suggest baseline testosterone and adrenal hormone concentrations, such as androstenedione and DHEAS, the sulfate ester of DHEA, are involved in maintenance and development of aggression and impulsivity in prepubescent boys (Azurmendi et al., 2006; Ramirez, 2003; Sanchez-Martin et al., 2011; Sánchez-Martín et al., 2000).

Despite this body of work, other studies have produced mixed results. For instance, a recent longitudinal study measuring developmental trajectories of children over a two-year study in 8–10-year-old children showed that boys', but not girls', levels of aggression increased over that two-year time frame, and that baseline cortisol and estradiol levels (but not testosterone) contributed to explaining this statistical effect (Azurmendi et al., 2016). In contrast, a previous study observed a significant relationship between testosterone and measures of aggression in the form of free play among preschool boys (Sánchez-Martín et al., 2000), while another study reported a significant effect between aggression and androstenedione only, not testosterone, in 5-year-old boys (Azurmendi et al., 2006). It is likely that different methodological approaches to measuring aggression (observational, survey, verbal versus physical expression) explain some of the variation in these findings. Other work has investigated children with conduct disorders who exhibit severe aggression and found that in comparison to controls these children had significantly higher levels of DHEAS and moderately higher levels of androstenedione, but testosterone levels did not differ (van Goozen et al., 1998; van Goozen et al., 2000). Despite the mixed results, these data suggest that testosterone and adrenal androgen concentrations are linked to the development and manifestation of aggression, with a focus on baseline concentration measures as a complement to studies of reactive hormone changes.

Observational studies provide initial support for the view that middle childhood represents a critical period to refine and practice for the sociocompetitive challenges of adulthood, as evidenced by the intensification of behavioral sex differences that become more pronounced during the juvenile transition (Benenson, 2014; Crittenden et al., 2013; Del Giudice et al., 2018; Geary, 2010; Herdt and McClintock, 2000; Konner, 2010). In biological terms, juvenility coincides with the growth stage in which an individual is still sexually immature, exhibits greater independence, and no longer relies entirely on their parental support unit for survival (e.g., Konner, 2010). In humans, this stage typically spans approximately 7 to 12 years, coincides with the onset of adrenarche, the pre-pubertal increase in adrenal androgen secretion of DHEA and its metabolite androstenedione, and is commonly referred to as middle childhood (Bernstein, 2016; Bogin, 1999; Campbell, 2011). However, there remains considerable variation in the timing of adrenarche between industrial versus non-industrialized societies, such that in non-industrialized populations, children tend to have a delayed onset in comparison to Euro-American averages (Helfrecht et al., 2018). Nonetheless, a key feature of modern humans is an unusually long juvenile period of growth and development that is distinct from closely related primates and similar-sized mammals (Thompson and Nelson, 2011). In the following sections, as an extension of the Challenge Hypothesis, we summarize work that investigated acute reactive steroid hormone responses and the emergence of sex-typed behavioral phenotypes during middle childhood.

On the basis of life history theory, the delayed reproductive maturity represented by an extended period of juvenile development in humans is hypothesized to represent a critical stage for intense social learning in preparation for the adult sociocompetitive environment (Del Giudice et al., 2009; Flinn et al., 2012; Meehan and Crittenden, 2016). Observational studies within industrial and non-industrialized societies suggest juvenility is a time of greater self-reliance and independence that coincides with the onset of sexual/romantic attraction and emergent sex-specific play patterned behaviors (e.g., higher rates of rough and tumble play in boys) (Benenson, 2014; Crittenden et al., 2013; DelGiudice, 2018; Geary, 2010; Herdt and McClintock, 2000; Konner, 2010). Despite the intensification of a suite of fitness-relevant sex differences in behavior during juvenility, few studies have investigated the potential activational effects steroid hormones may have on sociocompetitive behaviors in children before the onset of puberty. Further, little consideration has been given to hormone mechanisms that may be

distinct and adaptive for juveniles, at a time when testosterone is produced in low concentrations in comparison to adolescents or adult males (Nelson, 2005).

Recent work provides evidence that DHEA and androstenedione are sensitive to physically taxing male-male competition (Gray et al., 2017a; McHale et al., 2018a, 2018b, 2018c; McHale et al., 2016). Paralleling the adult testosterone and competition literature, sports participation among youth can be exploited as a naturalistic, ecologically valid, and viable context in which to investigate psychophysiological processes involved in individual and coalitionary aggression. Reactive hormone changes to competition can be evaluated by comparing salivary hormone levels before and after play. Recent work among boys, 8–11 years of age, in both US and Hong Kong samples, showed that DHEA increased during soccer practices, soccer matches involving only teammates (i.e., an intrasquad scrimmage), and during soccer matches against an unknown team of competitors (McHale et al., 2016; McHale et al., 2018a). Testosterone levels remained low and unresponsive, which differs from consistent findings reported among adult males engaged in rigorous forms of athletic competition (e.g., Geniole et al., 2017). In these same samples, androstenedione levels increased *only* during soccer matches involving unknown (out-group) competitors that were held in front of a moderate number of spectators, but did not significantly change during soccer matches involving peers (in-group). These findings suggest that androstenedione responses are sensitive to more meaningful forms of physical competition involving out-group competitors and spectators, whereas DHEA is likely responsive to the physical demands of competition more generally. Future work should explore the extent to which androstenedione may promote and/or be related to the developmental origins of ingroup and outgroup biases and aggression in additional contexts outside of juvenile physical competition.

In two other studies conducted in Hong Kong, no significant changes in DHEA, androstenedione, or testosterone were observed among boys during a moderately physically taxing, dyadic competition (table-tennis) involving peers or during a mixed-sex math competition (McHale et al., 2018b; McHale et al., 2018c). However, in the math competition, DHEA and androstenedione responses were significantly related to psychosocial variables: level of participation, and team performance. Due to the small sample sizes of the latter two studies (table tennis: $N = 22$ boys; math competition: $N = 45$, 18 boys) and familiarity of competitors in an informal competitive school setting, these results should be viewed with caution and demand a more robust methodological approach in the future (i.e., larger sample sizes, more meaningful competition in front of spectators), factors which have been consistently shown to influence acute testosterone responses in adult males (e.g., Geniole et al., 2017).

These findings lend preliminary support for the view that steroid hormone responses in juvenile children differ from those in adults engaged in similar forms of competition. Further, DHEA and androstenedione are capable of rapid increases during physical competition, fluctuate depending on the type of competitive contest and competitor type, and may be influenced by psychosocial variables, such as performance. These data provide additional evidence that testosterone may have a reduced role in aggression and competitive behavior in juveniles than in adults. By adjusting baseline and acute steroid hormone release in response to shifting reproductive demands across this life history stage, children exhibit behavioral and physiological flexibility while avoiding metabolic and fitness costs associated with immunosuppressive effects (i.e., down regulation) of maintaining chronically high levels of testosterone.

Comparative animal behavior evidence offers further insight into hormone regulatory processes that may have evolved in humans at life history stages when testosterone levels are low (e.g., middle childhood). For example, castration results in low levels of testosterone and yet does not reduce aggression in adult male prairie voles (*Microtus ochrogaster*) (Demas et al., 1999). Findings on male song sparrows (*Melospiza melodia*) and Siberian hamsters (*Phodopus sungorus*) during the non-breeding season, when gonads regress and testosterone levels plummet, has shown that the brain is capable of locally synthesizing sex steroids independent of circulating gonadal androgens in response to territorial aggression (Pradhan et al., 2010; Scotti et al., 2008; Wingfield et al., 2002). Among male song sparrows, rapid local synthesis of DHEA and androstenedione has been detected in the telencephalon following antagonistic encounters (Pradhan et al., 2010). Similarly, high circulating levels of adrenal DHEA in Siberian hamsters have been observed during the nonbreeding season, raising the possibility that adrenal hormones are an important regulator of aggression by serving as a precursor for the conversion of androstenedione (Scotti et al., 2008). Lastly, in Siberian hamsters and in adult mice, adrenalectomy is linked to a reduction in aggression, further providing evidence that adrenal hormones have important regulatory effects in rodents (Demas et al., 2004; Paterson and Vickers, 1981). Cumulatively, this research reveals that the dynamics of steroid hormone regulation of territorial behavior and aggression is less straightforward than previously assumed, can differ depending on the life history stage of an organism, and likely reflects adaptive life-history tradeoffs (Wingfield et al., 2018). Thus, our speculative interpretation of these cumulative findings is that baseline and reactive DHEA and androstenedione concentrations in human juveniles have the potential to influence immediate and future responses to social competition, such as aggression, during prepubertal development.

12. Life history extensions of the Challenge Hypothesis: senescence (aging)

Although the Challenge Hypothesis was originally proposed to explain testosterone levels in reproductive-aged males, it can be extended to a wider age span of adult males subject to reproductive senescence. Senescence refers to loss of function, and is tied into increasing age itself but intersected by risk factors such as acute and chronic health conditions and changes in social behavior (Crews, 2007). Life history theory anticipates for sexually reproducing species subject to indeterminate growth and some degree of unpredictable and inevitable extrinsic mortality that the body (soma) will deteriorate in function with advancing age (Jones et al., 2014; Kirkwood, 2002). The disposable soma (Kirkwood and Holliday, 1979) and antagonistic pleiotropy (Williams, 1957) theories formalize this logic. Organizational effects of testosterone perinatally and peripubertally support adult male mating effort through such allocations as muscle maintenance and competitive and courtship behavior, but have downstream costs that lead to reduced later-life survival (Bribiescas, 2017; Kruger and Nesse, 2006).

The pace of human senescence has slowed, yielding longer maximum lifespan and higher survival at later ages compared with great apes such as chimpanzees, gorillas, and orangutans (Gurven and Kaplan, 2007; Wood et al., 2017). There is much debate about the primary drivers of extended human lifespans. Some models focus on benefits of extended maternal survival (“mother hypothesis”: Peccei, 1995) for offspring success, grandmaternal survival and investment on grandchildren's success (“grandmother hypothesis”: Hawkes et al., 1998; Hawkes and Coxworth, 2013), and benefits to extended male lifespans through direct reproduction (“patriarch hypothesis”: Marlowe, 2000b). Deeper discussion of the evolutionary causes of extended human lifespans is outside the present scope. That said, human male behavior exhibits what can be deemed reproductive senescence. Measures of male physical competition such as athletic prowess (e.g., age profiles of most competitive athletes in sports such as running: Berthelot et al., 2012), violent crime (Laub and Sampson, 2001), spontaneous aggression resulting in homicide (Daly and Wilson, 1988), and establishing status based on social dominance (rather than freely conferred prestige: Simmons, 1945) decrease with age.

Measures of individual (e.g., masturbation) and partnered (e.g., intercourse) sexual behavior decrease with advancing age (DeLamater,

2012; Gray and Garcia, 2012; Gray et al., 2019) (DeLamater, 2012; Gray and Garcia, 2012; Gray et al., 2019). In addition to lower mating effort, men more often become invested in long-term partnerships that may yield children or grandchildren to whom they provide services such as protection, resources, direct care, or knowledge (Bribiescas, 2017; Bribiescas and Burke, 2017; Gray and Crittenden, 2014). In other words, age-specific demographic profiles of male fertility and grandparenting indicate that mating effort often shifts to parenting (or grandparenting) effort (Shwalb and Hossain, 2017). Besides behavioral measures, other traits similarly evidence human male reproductive senescence: changing body composition (e.g., reduced muscle and increased fat), motivation (e.g., reduced sexual desire), erectile function, sperm quality and quantity, cardiovascular function, etc.

Within the scope of the Challenge Hypothesis, age-related changes in baseline functioning of the human male hypothalamic-pituitary-gonadal (HPG) axis can be viewed as putatively adaptive. Testosterone levels tend to begin declining in men in their 30s or 40s, with most cross-sectional and longitudinal studies pointing toward slow decreases thereafter. Humans living in energetically constrained ecologies that include food constraints, high physical activity, and high infectious diseases burdens have lower baseline testosterone levels than men in less energetically constrained ecologies, such as US cities (e.g., Ache of Paraguay: Bribiescas, 1996; Ariaal agropastoralists of Kenya: Gray et al., 2007; Tsimane forager-horticulturalists of Bolivia: Trumble et al., 2012; Hadza foragers and Datoga pastoralists of Tanzania: Muller et al., 2009). The lower baseline testosterone levels of men in more energetically constrained contexts results in diminished age-related testosterone decreases, in good part because young men's testosterone is lower and thus has less far to fall with advancing age (Ellison et al., 2002). Migration research also shows that early childhood energetic environment shapes variable adult baseline testosterone levels, with higher testosterone levels found among men who migrated to England in adulthood following early life in Bangladesh compared to men who remained in Bangladesh through adulthood (Magid et al., 2018).

Almost no research has explicitly tested whether the magnitude of men's testosterone responses to competitive challenges, sexual opportunities, or caregiving encounters changes with advancing age. Considering life history theory and reproductive senescence in the context of the Challenge Hypothesis, one might hypothesize that older men will show reduced testosterone responses to same-sex competitive and sexual stimuli. Moreover, older men (with lower baseline testosterone) might be more drawn toward children and grandchildren, with potential for affiliative and intensive interactions with young children to reduce men's testosterone. In a study of adult men visiting a sex club, age was not related to the magnitude of men's testosterone response to sexual exposure (Escasa et al., 2011); this is contrary to the expectation that testosterone reactivity to sexual stimuli in aging men should decline due to decreasing mating effort. Among men engaged in heavy resistance exercise, older men had lower testosterone responses than younger men (Kraemer et al., 1998). More attention to age as an independent variable predicting testosterone responsiveness is warranted and based on expectations of shifting male life history allocations.

A large and growing industry focuses on prescription testosterone treatment (PT) among aging men, with its greatest impact in the U.S. (Gabrielsen et al., 2016; Rao et al., 2017). This industry has inspired randomized double-blind placebo-controlled trials to quantify risks and benefits of testosterone therapy among older men, also yielding causal insight into the effects of testosterone on key phenotypes such as sexual desire and behavior (Bhasin et al., 2018). The clinical literature on testosterone operates distinctly from human behavioral endocrinology and life history literatures (for an exception, see Ivanov et al., 2018). Findings between life history theory, reproductive senescence, and clinical testosterone trials might be integrated within an extended scope born from the Challenge Hypothesis.

One key consideration is whether “low testosterone” is a problem among older men warranting treatment with prescription testosterone, or instead reflective of non-problematic diminishing life history maintenance pressures (i.e., reproductive senescence). There are debates in the clinical literature about a potential testosterone threshold that might be deemed “low” and which symptoms are correlated with this threshold (Aversa and Morgentaler, 2015; Bhasin, 2018; Mirone et al., 2017). The attempt to identify a single threshold distinguishing low (“hypogonadal”) and normal (“eugonadal”) testosterone level ignores population variation in testosterone levels and the many contributors to establishing what is a “normal” range in the first place. The optimal way to measure testosterone is itself debated by clinicians, and quite sophisticated compared to the early technical capacity that made measurement of serum testosterone in field studies possible. Optimization includes attempts at lab assay standardization, sample collection standardization (e.g., multiple fasting morning blood samples) and consideration of key patient “covariates” such as diabetes status and/or medications like opioids (Bhasin et al., 2018). Testosterone can be administered in a variety of formulation (e.g., gel, patch, injection). An ideal target for elevated testosterone is often specified as the mid-normal testosterone range for young men (low: 230–350 ng/dl; median normal: 698.8) (Bhasin et al., 2011; Tsametis and Isidori, 2018). From the standpoint of the Challenge Hypothesis, one might frame clinically-based elevations in aging men's testosterone as potentially altering responsiveness to competitive challenges, sexual opportunities, and care of young children.

The clinical literature provides insight into the effects of exogenous testosterone on older men's sexual function. A 2014 meta-analysis on testosterone therapy and sexual function concluded that PT had positive effects on sexual function in hypogonadal subjects but its effects on eugonadal subjects remained unclear (Corona et al., 2014). A systematic review and meta-analysis of randomized placebo-controlled PT trials revealed that testosterone, relative to placebo, predicted improvements in libido, erectile dysfunction (ED), and sexual satisfaction among hypogonadal (but not eugonadal) men (Ponce et al., 2018). Results from the Testosterone Trials (a multi-center US set of testosterone trials involving elderly men with low testosterone) suggested that, compared to placebo, PT increased all aspects of sexual activity and libido, although its effect on ED was weaker. Moreover, Snyder et al. (2016) found levels of sexual activity and libido were associated with incremental increases in serum testosterone levels, but ED showed no association. Overall, the above studies and reviews suggest that PT can improve sexual activity and libido in hypogonadal men, but further studies are necessary to understand its potential effects on sexual desire and behavior in patients with normal testosterone levels.

If exogenous testosterone influences men's mood and cognition, this could be indirectly relevant to mating effort (e.g., enhanced energy might foster engagement in competitive encounters at work or perhaps more involvement in family life). However, the effects of testosterone therapy on energy and cognition are unclear. The Testosterone Trials (reviewed in: Bhasin et al., 2018) found no significant improvements in cognition after treatment, despite a small prior study's claims of positive effects on spatial and verbal memory for older men (Snyder et al., 2018). Evidence is mixed on the effects of testosterone therapy on mood. PT weakly improves overall mood (which can be measured via a set of scales based on negative moods such as anger, in addition to positive mood parameters such as alertness and friendliness), but the magnitude of this effect on older men was small, and success in treating diagnosed depression and depressive symptoms seems limited (reviewed in Bhasin et al., 2018). Lašaitė et al. (2017) found no improvements in emotional state or quality of life after two years of testosterone treatment in a small sample of young and middle-aged hypogonadal men. Finally, neither the Testosterone Trials nor a commissioned systematic review and meta-analysis found improvements in energy (measured as fatigue) versus placebo (Bhasin et al., 2018; Snyder et al., 2016). Other studies in younger men have found few benefits of testosterone on depression, cognition, energy and mood (Amore et al., 2012; Holland et al., 2011; Seidman and Weiser, 2013),

but are contradicted by work on older men showing positive effects on depression, quality of life, and cognition (Hackett et al., 2013; Jung and Shin, 2016; Nian et al., 2017).

As a complement to research that seeks to measure effects of prescription testosterone in placebo-controlled trials, one of our recent studies has sought to directly ask men taking prescription testosterone to characterize the reasons they elected to take testosterone and its perceived effects, guided by core open-ended questions (Straftis and Gray, in review). In an online survey of 105 US men aged 21 and older, the most commonly specified reasons for initiating prescription testosterone were "low testosterone" (39 cases), well-being (37 cases), energy (30 cases), libido (23 cases), social energy (20 cases), fat (19 cases), and other/miscellaneous (19 cases). Split by men aged forty years and older vs. men younger than 40 years, older men were much more likely to specify libido as a reason for taking testosterone. The most commonly identified perceived benefits of prescription testosterone were energy (55 cases), libido (44 cases), muscle (30 cases), other/miscellaneous (27 cases), fat (19 cases), well-being (19 cases) and social energy (18 cases), with none of these perceived benefits differing for men older vs. younger than 40 years of age. These men on prescription testosterone were looking for a fountain of well-being, energy and sexual desire, increased muscle mass, and decreased fat. It may be that these men sought to engage in more social competition/sexual interaction than they did during their self-reported "low testosterone" state; framed within the Challenge Hypothesis and life history theory, these men sought to enhance facets of mating effort and somatic maintenance.

Respondents in this same online survey were also asked to describe changes in either their work motivation or family life after taking prescription testosterone. Of those who responded ($n = 97$) to "since taking prescription testosterone, have you noticed any changes in your motivation at school/work?" $n = 78$ (80.41%) claimed they noticed effects, and 98% claimed those effects were positive. The most frequently coded themes among those who reported changes in motivation were social energy (32 cases), energy (31 cases), and focus (17 cases). When presented with "please describe any changes you have noticed in your family life, since taking testosterone", 58% of men ($n = 61$) reported positive effects due to testosterone, whereas the remainder either responded with negative effects or "n/a". The positive family effects were typically couched in terms of energy, social energy, or libido. An interpretation of the high prevalence of energy and social energy is that men seek/perceive benefits of more active engagement with their world, including the competitive and cooperative dimensions of their social world. We suspect that there is a signal in this energy/social energy of enhanced male social dominance that is subtle compared with more overt forms of same-sex physical aggression.

We also highlight that most men perceived favorable effects of testosterone on their family life (Straftis and Gray, in review). At face value, this conflicts with the idea framed by the Challenge Hypothesis that elevated testosterone might compromise parental behavior. If a biomedical model of testosterone and family life were developed, it would suggest that if low testosterone is linked with low mood and diminished social engagement, then an elevation in testosterone might foster better male engagement with his family. Our survey findings support the latter model better, highlighting the importance of incorporating measures of partner dynamics and childcare in evaluations of the effects of exogenous testosterone in men. Moreover, such potential effects of exogenous testosterone on family life warrant more cross-cultural attention, given that aging men exhibit a range of behaviors from extensive fathering/grandfathering to aloofness (Shwalb and Hossain, 2017; Shwalb et al., 2013).

Among some men treated for advanced prostate cancer, testosterone is reduced via androgen deprivation therapy (ADT), amounting to chemical castration. From the standpoint of the Challenge Hypothesis, ADT might be expected to yield reduced interest in social competition, courtship, and sexual behavior, but perhaps more sensitivity to young children. Observational studies of older men on ADT have pointed to negative consequences for bone maintenance, muscle loss, increased risk of gynecomastia, increased anemia, decreased energy, diminished sexual desire and erectile function, and hot flashes, among other effects (Donovan et al., 2015; Elliott et al., 2010; Nguyen et al., 2015). These findings are almost entirely restricted to North America or Europe, however, so may be of limited applicability in wider sociocultural variation. Nonetheless, the prominent impacts on sexual function within partnerships underscore the relevance of testosterone to older men's social behavior, and how experimental decrease of testosterone in that relationship context can have deleterious consequences. Testable hypotheses born from the Challenge Hypothesis are that men on ADT will show reduced interest and success in same-sex social competition (men who experience reduced energy may feel it most relevant in social circumstances), in addition to reduced interest in seeking a new mate.

13. Costs of testosterone

In the original Challenge Hypothesis paper, Wingfield et al. (1990) presented a section entitled "Costs of High Testosterone Levels." The authors highlighted elevated predation risk to males and their offspring, energetic costs, and potential costs to parental care. The latter potential cost draws upon the role of testosterone as a regulator of male allocations to competing mating and parenting efforts, as discussed previously. In a subsequent review, Wingfield et al. (2001) added to these costs of testosterone, also pointing to oncogenesis such as prostate cancer, weakened immune systems, interference with pair bonds, decreased fat, increased risk of injury, and higher mortality. A body of research expands on the Challenge Hypothesis, life history theory, and evolutionary biology to address the costs of testosterone.

Natural selection favors reproductive success rather than survival, resulting in potential life history tradeoffs between reproductive effort and maintenance (survival). This is most dramatically represented in studies evaluating effects of castration on male lifespan. While a small study failed to find differences in lifespan between castrated male singers and controls in historical Italy (Nieschlag et al., 1993), other studies of Kansas inhabitants of a mental care facility (Hamilton and Mestler, 1969) and historical Korea found that castrated men lived longer than intact men (Min et al., 2012). Studies of chemically castrated men (e.g., men on ADT) may also illuminate the costs of testosterone, such as testosterone promoting prostate tumors. In contrast to these findings of mortality benefits of low testosterone within a life history framework, the clinical and epidemiological literature tends to view low testosterone among aging men as a risk factor for illness or death (Holmboe et al., 2018; Shores et al., 2012; Yeap et al., 2014), perhaps in part because low testosterone is a marker of poor health.

Testosterone appears to both reflect and modulate investment in reproductive effort, particularly mating effort, potentially at a cost of investments in maintenance functions such as immune function (Muehlenbein and Bribiescas, 2005). How strong are the links between testosterone and compromised immune function? In a meta-analysis of 166 studies of both nonhuman taxa and humans, significant negative effects of experimentally increased testosterone on male immune measures were found, with an overall effect size of −0.28 [95% CI: −0.39, −0.17] (Foo et al., 2017). Among 120 correlational studies, however, there was no significant relationship between circulating male testosterone and immune function measures. Much of this research was inspired by the immunocompetence handicap hypothesis (ICHH), which states that the (immune) costs of supporting high testosterone result from honest sexual signals sent by males of high phenotypic quality (Folstad and Karter, 1992). One interpretation of the meta-analysis findings is that causal evidence of the effects of testosterone can be identified only in experimental manipulations. Moreover, in nonhuman primates, as likely among other taxa including humans, null relationships between in vivo testosterone and immune measures may be due to a host of factors, including the energetic status of focal

subjects, social environment, immune measures (e.g. parasite load), and other elements of research design (Prall and Muehlenbein, 2014). Alternatively, testosterone may exert more specific immunomodulatory effects on immune function (Braude et al., 1999), rather than across-the-board suppressive effects. In this more specific immunomodulatory model, testosterone promotes immune functions that may aid in responding to injuries resulting from male-male physical aggression at the expense of other immune functions, such as t-cell production.

Wingfield et al. (1998) advanced the concept of the "emergency life history stage" to address extreme and chronic stressors eliciting a physiological (e.g. an elevated glucocorticoid response and lower levels of sex steroids) and behavioral response. Another way to frame an immediate life history challenge to an organism is as a threat to survival, resulting in prioritization of maintenance functions at expense to reproductive allocations. We highlight several such cases in which decreased testosterone can be interpreted as a consequence of prioritized maintenance function in the face of a short-term threat to survival. The first of these relates to immune function challenges: in the face of acute illness, the body may respond by decreasing testosterone levels. In a review of human responses to sickness, Shattuck and Muehlenbein (2015) observed that male testosterone regularly decreases in the early stage of response to sickness and trauma, then increases during recovery. As examples, testosterone levels were lower among men in Honduras during an acute response to malaria before rising with recovery (Muehlenbein et al., 2005), and in other work were found to be lower among men with HIV, sleeping sickness, and other infections (Shattuck and Muehlenbein, 2015).

Other lines of evidence align with prioritization of survival over testosterone and reproductive effort in the face of major anabolic challenge. In a study of 23 young men, Trumble et al. (2010) showed that skipping a single evening meal resulted in lower subsequent morning testosterone. Shortened sleep duration can decrease men's testosterone (Axelsson et al., 2005), with REM sleep appearing to drive pulsatile testosterone release. Men deprived of sleep had lower testosterone and scored lower on a lab-based test of aggression (Cote et al., 2013). High amounts of physical activity such as long-distance running (Hooper et al., 2017; Wheeler et al., 1984) or rigorous military training (Gomez-Merino et al., 2005; Morgan et al., 2000) can decrease men's testosterone. Among 66 male ultramarathon runners, testosterone decreased after compared to before the race, whereas two measures of innate immune function (hemolytic complement activity and bacterial killing ability) increased; moreover, men's arousal scores to provocative female images decreased, consistent with an acute life history focus on survival over reproduction (Longman et al., 2018).

14. Synthesis of the Challenge Hypothesis, life history, and human research at 30 years

The Challenge Hypothesis has helped stimulate a considerable amount of human research. The citation analysis evidenced patterns in this human research literature. The sections on competition, sexual behavior, partnering, and parental behavior also capture key contours in this body of research. There are recurrent variables, such as those related to context and personality, that are associated with levels of baseline and reactive testosterone in primarily male but sometimes also female social behavior. Fig. 2 serves as a conceptual integration of these patterns. One of the primary extensions depicted in this Figure and represented in the present review is the adoption of a life course perspective. Another take-away message is that the sizable amount of human empirical research framed by the Challenge Hypothesis is still expanding.

The body of human Challenge Hypothesis and life history research has drawn upon, and informs, a variety of research designs. The Challenge Hypothesis was inspired by naturalistic, correlational field data from birds, but has expanded in various directions as other contributions in this special issue indicate, including experimental modulation of testosterone to determine effects on social behaviors. Most human studies are observational and enable testing associations between either baseline or reactive testosterone and independent variables such as demographic status (e.g., marital status) or other variables (e.g., age, motivational measures). A relatively smaller subset of studies are longitudinal, and enable determining causality over time such as how a change in some social variable like marital status may change a man's testosterone level. Studies conducted in labs enable more social experimental control, whereas naturalistic study designs benefit from ecological validity but often yield "noisier" data. The human literature thus harbors both some similar emphases in research design (e.g., many field studies of testosterone and male family life) as the original Challenge Hypothesis, but is complemented by lab-based studies in which a social variable's effect (e.g., courtship encounter or exposure to baby stimuli) on testosterone can be isolated. A relatively recent addition to studies in humans has been to test effects of one-time testosterone administration on relevant phenotypes such as competition. While many men undergo experimental modulations (e.g., PT and ADT) of their testosterone in clinical contexts, rarely have consequences of those interventions been integrated with expectations or interpretations framed by the Challenge Hypothesis.

After thirty years, many directions for future research remain. Among juveniles, research could continue to refine how context, personality traits, and other factors influence DHEA and androstenedione responses. A key question is what any such baseline and reactive changes in adrenal androgens might mean, with research on steroid hormone receptor distribution and brain imaging in humans and non-human juveniles helping to determine the roles of adrenal androgens. A life course approach also invites one to ask how adrenal androgen responsiveness among juveniles might predict later-life social behaviors, including success in competition. Among adults, both in prime reproductive age and in senescence, future research could address how experimentally increased testosterone influences care of children and potentially grandchildren. The Challenge Hypothesis suggests that experimentally elevated testosterone will inhibit paternal care. However, effects of testosterone on direct nurturant care might be quite distinct from paternal protection or provisioning, and the findings that older men on prescription testosterone generally expressed favorable (rather than negative) effects on family life goes against a straightforward extension of the Challenge Hypothesis. Humans also regularly live long enough for men to provide care as grandfathers to their descendants, and yet there have been no studies testing whether nurturant grandpaternal care is associated with reduced testosterone.

Experimental social interventions offer avenues for future research. Relatively little research, as noted above, has tested whether men respond to courtship challenges with increased testosterone, with such challenges perhaps most salient in young adult years during peak mating effort and social contexts characterized by many male competitors and more available potential mates. Although theory might anticipate decreased magnitude of testosterone responses to social competition and courtship with advancing age (less somatic support for mating effort), little hormonal research enables testing this, despite existing behavioral research (e.g., in same-sex homicide rates) suggesting age should itself be viewed as a salient independent and life history variable. Men on PT or ADT should also have blunted testosterone responses compared to control men, suggesting that (for example) a man on PT may exhibit a blunted testosterone response to a courtship encounter relative to a control man. Incorporation of ecologically valid life history costs to men's testosterone responses to social variables suggests that when men are sick or sleep deprived (as examples), they too should exhibit less pronounced testosterone responses to same-sex competitors or courtship than when those same men are recovered from such contexts. As the Challenge Hypothesis celebrates this 30-year landmark, these are among the many avenues awaiting continued research inspired by the recognition that social context and life history shape human testosterone variation.

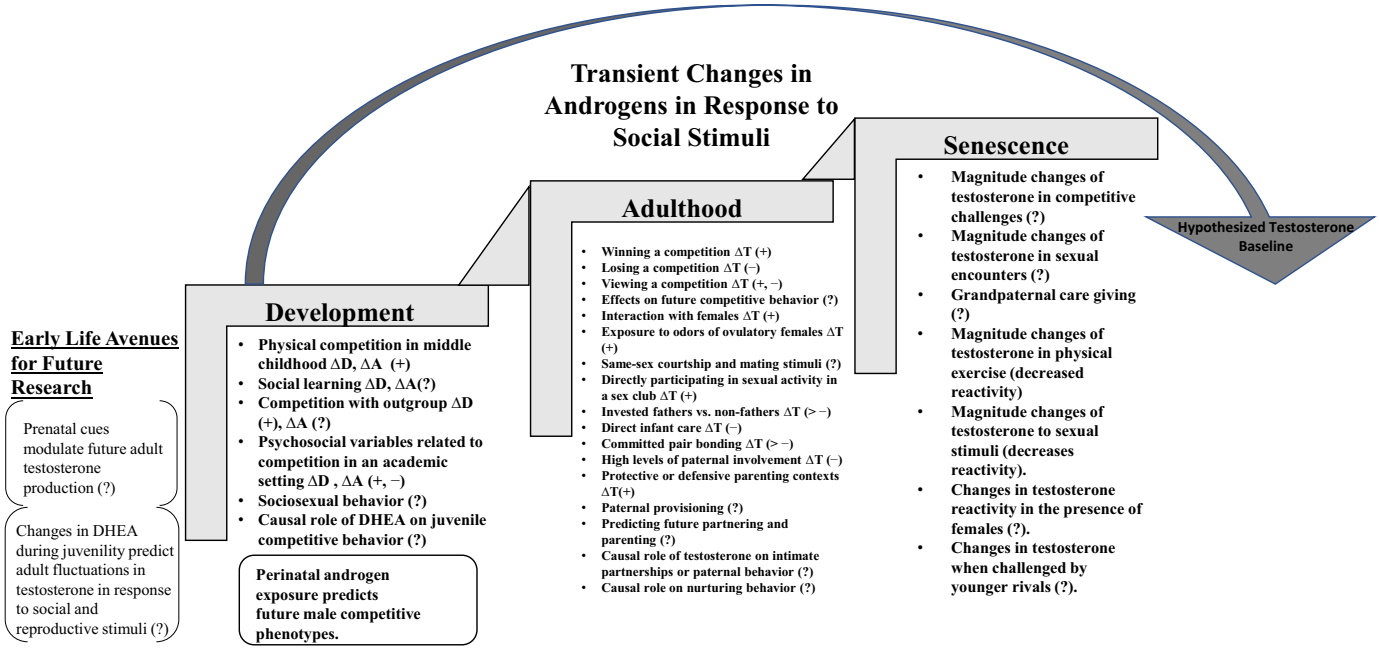

Fig. 2. Reproductive Behavioral Domains and the Challenge Hypothesis Across the Male Life Course. Tested male hormone responses for transient change in testosterone (ΔT), change in DHEA (ΔD), change in androstedione (ΔA). Positive (+) signifies increase. Negative (−) signifies decrease. Greater than indicates greater decrease (> −). Question mark (?) indicates a need for further research efforts . The large curved arrow indicates hypothesized breeding baseline change in testosterone over the male life course.

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