Stress and Androgens in Himba Women

Article in Adaptive Human Behavior and Physiology · October 2023

DOI: 10.1007/s40750-023-00227-w

CITATIONS

CITATIONS

O

READS

28

3 authors, including:

Sean Prall
University of Missouri
42 PUBLICATIONS 701 CITATIONS

SEE PROFILE

SEE PROFILE

SEE PROFILE

READS

AREADS

AREADS

AREADS

AREADS

AREADS

AREADS

BREADS

AREADS

A

RESEARCH



Stress and Androgens in Himba Women

Sean Prall¹ ⋅ Brooke Scelza² ⋅ Benjamin C. Trumble^{3,4}

Received: 16 July 2023 / Revised: 2 October 2023 / Accepted: 3 October 2023 © The Author(s), under exclusive licence to Springer Nature Switzerland AG 2023

Abstract

Purpose Adrenal androgens like dehydroepiandrosterone (DHEA) are important to numerous aspects of health and psychosocial stress physiology. DHEA is responsive to stress, and previous studies have shown chronic stress can be associated with a reduction in DHEA. However, the large majority of this work has been conducted in resource-rich, industrialized societies, with few studies examining how adrenal androgens respond to stressors in environments with persistent resource related concerns. Here we examine the relationships between androgens and chronic psychosocial stress in a sample of Himba pastoralists, in order to determine the relationship between DHEA and stress in a resource-limited environment.

Methods We assayed DHEA and testosterone in 122 afternoon saliva samples from 46 Himba women aged 18–66, median age 30. Women also completed a chronic psychosocial stress survey, which included social, health, and resource related stressors reported over the past thirty days.

Results DHEA concentrations show a curvilinear relationship with age, peaking in the mid-30s; testosterone was relatively flat across the life course. DHEA, but not testosterone, was negatively associated with chronic stress scores. In a comparison of question types, resource-related stressors showed the strongest relationship with DHEA.

Conclusion Our results support findings from previous studies conducted in industrialized societies, showing that chronic stress is associated with a reduction in DHEA concentrations. In contrast, salivary testosterone appears unrelated to chronic stress. Given the associations between DHEA and other aspects of health, better understanding of drivers of DHEA variability can elucidate linkages between stressors and health outcomes.

Published online: 17 October 2023

Center for Evolution and Medicine, Arizona State University, Tempe, AZ, USA



Sean Prall sprall@missouri.edu

Department of Anthropology, University of Missouri, Columbia, MO, USA

Department of Anthropology, University of California Los Angeles, Los Angeles, CA, USA

School of Human Evolution and Social Change, Arizona State University, Tempe, AZ, USA

Keywords Stress · Androgens · DHEA · Testosterone · Pastoralist · Himba

Introduction

Chronic psychosocial stressors can fundamentally alter endocrine physiology, with important implications for health and wellbeing (McEwen, 2007). Understanding variation within and between populations in how chronic stress can alter hormone profiles may help us to better understand how and why chronic stress is linked to health disparities. A host of physiological systems help the body respond to short-term stress, coordinating heart rate, blood pressure, immunological, and metabolic actions to make crucial adjustments that allow organisms to respond to changing conditions and threats to survival. However, at longer time intervals, these processes can have detrimental impacts on the same physiological systems (Bauer et al., 2009; Juster et al., 2010; McEwen, 2007). The hypothalamic-pituitary-adrenocortical (HPA) axis is centrally involved in regulating endocrine responses, producing catecholamines and adrenal androgens that have potent effects on health and cognition (McEwen, 2007; Pluchino et al., 2015; Quinn et al., 2018). Dysregulation in the production of these hormones has been implicated in physiological and psychological disfunction (Joseph & Golden, 2017; Klinge et al., 2018; Lupien et al., 1994).

The adrenal androgen dehydroepiandrosterone (DHEA) and its sulfated metabolite DHEA-S (together DHEA/S) are responsive to HPA activation (Dutheil et al., 2021). Experimental paradigms indicate marked increases in DHEA/S following acute stressors (Izawa et al., 2008; Prall et al., 2017). Similarly numerous studies, primarily in the context of social or work stress, indicate that chronic stress fundamentally alters adrenal androgen profiles, lowering DHEA/S concentrations (e.g. Lennartsson et al., 2013a, b). To date, these studies have only been conducted in industrialized populations with chronic stressors such as occupational stress that may not translate well into non-industrialized contexts. Other more ecologically valid stressors, like resource stress (e.g. food insufficiency, money insolvency, lack of access to medications or clean water), may better represent the types of psychological and physiological burdens experienced throughout our evolutionary past, and may be more culturally relevant in subsistence based societies.

DHEA and DHEA-S are synthesized in the zona reticularis of the adrenal cortex in large quantities under stimulation from adrenocorticotrophic hormone (ACTH). Synthesis of DHEA/S peaks in early adulthood before a decline with senescence (Davison et al., 2005; Orentreich et al., 1984). The primary function of these hormones is thought to be as precursors to downstream steroids, but DHEA has its own effects on several physiological systems independent of its role as a precursor (Traish et al., 2011). These actions may be mediated through its function as an intracrine hormone, or through direct effects of several receptors and physiological pathways (Clark et al., 2018). As a prohormone with its own independent diverse interactions and effects, teasing out the direct implications of DHEA variation from confounding factors remains a challenge. However, DHEA/S responses to acute stress are well documented, echoing cortisol spikes. ACTH from the anterior pituitary, in response to CRH binding, kickstarts the enzymatic cascade to synthesize



DHEA/S and cortisol. The majority of DHEA/S is synthesized in the adrenals, but the brain, ovaries, and testes produce an estimated 20% of these androgens (Labrie et al., 2011). Unlike cortisol, DHEA/S doesn't exert negative feedback on the HPA axis. Additionally, DHEA/S has been shown to exert anti-glucocorticoid-like effects, meaning it's simultaneously being stimulated by HPA activation, while blocking some actions of HPA activity. Chronic exposure to high levels of cortisol is well known to have significant negative health impacts (McEwen & Stellar, 1993), and the opposing action of DHEA has been shown to ameliorate these impacts. In the brain, DHEA/S ameliorates the impact of glucocorticoids neuron activity and function (Cardounel et al., 1999; Karishma & Herbert, 2002; Kimonides et al., 1999). Similarly, DHEA/S plays a role in altering immune function, including pathways that are disrupted by excessive cortisol activity (Hazeldine et al., 2010; Prall & Muehlenbein, 2018). As a result of these activities, many have hypothesized that the relative concentrations of DHEA to cortisol are important in determining health outcomes, particularly under chronic stress exposure (Markopoulou et al., 2009; Phillips et al., 2010).

Despite clear increases in DHEA/S in response to acute stress (Dutheil et al., 2021), chronic stressors can result in lower levels of adrenal androgens under some conditions. Early primate studies indicate that these changes can occur fairly quickly, with only three days of stress resulting in significant reductions in DHEA (Mason et al., 1968). Work stress or chronic stress as a result of being a caregiver is associated with lower DHEA-S (Arnetz et al., 2019; Jeckel et al., 2010; Lennartsson et al., 2013a, b). These baseline differences in androgen profiles impact acute stress responses, resulting in blunted DHEA-S responses to acute stressors, but not changes in DHEA, cortisol, or ACTH (Lennartsson et al., 2022, 2013a, b). However, other chronic stressors such as being unemployed or experiencing bullying at work are associated with higher baseline DHEA/S (Gallagher et al., 2016; Lac et al., 2012), and DHEA-S has been negatively correlated with anxiety and depression (Brzoza et al., 2008). Chronic stress is generally associated with reduced DHEA/S in workplace settings, but these findings are mediated by type and duration of stressors.

Bouts of acute and chronic stress can have complex interactions with the production of other androgens like testosterone, dependent on physical condition, compensatory stimulation, type and duration of the stressor, individual traits and social dynamics, and the production of other hormones (Chichinadze & Chichinadze, 2008; Wingfield & Sapolsky, 2003). While exercise can cause acute increases in testosterone concentrations (Vingren et al., 2010), studies of stressors and gonadal androgens have indicated demonstrable reductions in testosterone in men in response to conditions including endurance exercise, stressful training programs, to massive loss in resources (Daly et al., 2005; Kreuz, 1972; Trumble et al., 2018). Women produce testosterone from the adrenal glands and ovaries levels 15-fold lower than adult men (Handelsman et al., 2018), and concentrations decline with age (Davison et al., 2005). Like men, women's testosterone production is responsive to social stimuli (Goldey & Van Anders, 2015; van Anders, 2013). Less is known about the relationship between stress and testosterone in women. Testosterone shows acute increases in response to a laboratory stressor in both men and women (Lennartsson et al., 2012). Testosterone is reactive to athletic competition, but women with higher



baseline cortisol show lower testosterone reactivity to a competitive event (Edwards & Casto, 2015). Similarly, women who report more martial conflict have lower testosterone (Gettler et al., 2019). However, chronically stressed women have higher overnight urinary testosterone than unstressed women in one study (Powell et al., 2002). Conversely, exogenous testosterone can decrease HPA responsiveness (Hermans et al., 2007). These complex relationships between androgens and stressors in women are relatively understudied, in part because of fundamental assumptions about the role of testosterone and masculinity, which may discount the importance androgens in women (van Anders, 2013).

The goal of this study is to better understand the role of social and ecological stressors on androgen production in women. In particular, we are interested exploring the relationships between self-reported chronic stress and basal levels of salivary androgens outside of industrialized settings, including stressors that may be more ecologically valid. We utilize a locally developed measure of chronic stress, with questions were designed to be more culturally salient. More broadly, there is little documentation of adrenal androgen age profiles outside of non-industrial populations, and little appreciation of cross-population variation. DHEA in particular has long been implicated in health outcomes, healthy stress responses, and healthy aging. Documenting inter-population age differences in DHEA and testosterone profiles can elucidate social and ecological drivers of androgen production and downstream impacts on health.

Methods

Study Community

This study was conducted as part of the Kunene Rural Health and Demography Project, a longitudinal study of health, reproduction, and family life among Himba agropastoralists in northern Namibia. Namibia has one of the highest levels of inequality in the world, and the Kunene region (where our study is focused) is notable for having one of the lowest human development scores and highest levels of inequality in the country (NHDR, 2019). Himba, in particular tend to fall at the bottom of these rankings, as this population has long experienced social and economic marginalization, described by Bollig (1998) as "colonial encapsulation." This included restrictions on livestock sales and land tenure, which have contributed to Himba continuing to have limited access to the cash economy. Access to healthcare is also limited in this area, with the closest clinic a full day's walk for most of the people in our study area, and only one regional hospital, which is more than 150km away.

As this study focuses on women, we will concentrate our ethnographic description on women and women's gender roles and experiences. Additional details on Himba men, families, and reproductive dynamics can be found elsewhere (Bollig, 2006; Prall & Scelza, 2020a; Scelza et al., 2019, 2021). Himba live in polygynous households of 5–25 individuals centered around a senior head-of-household. Families are polygynous, with each co-wife having her own hut and cooking fire, and access to a proscribed portion of the household herd for milking. The individuals in



our study area rely on a subsistence-based diet, with limited access to the cash economy. Their diet consists mainly of milk, meat, and maize (with occasional supplementation of store-bought foods). Women are responsible for most household level tasks outside of herding, including milking animals, cooking, growing and processing garden crops in matrilineally owned gardens, collecting and carrying water, and childcare. This region of the country is prone to frequent and prolonged drought, which is a cause of resource stress and loss of livestock (Prall & Scelza, 2023). Himba women have a high degree of reproductive autonomy and freedom of mobility (Scelza et al., 2019). Most Himba men and women have multiple concurrent romantic partners, a practice which has been linked to greater access to resources for women and a better ability to buffer against resource stress (Prall & Scelza, 2020b; Scelza et al., 2020, 2021).

Saliva Collection

All samples were collected in July and August of 2017. Study participants (n=46women, aged 18-66, median age of 30) collected approximately 2 mL of saliva via passive drool into a 5 mL cryovial. To minimize the impact of diurnal variation on androgen levels, saliva samples were collected between 3PM and 6:30PM. This timeframe corresponds with the nadir of diurnal levels of testosterone, and has been used in similar contexts to assess relationships between androgen levels and social dynamics (Gettler et al., 2014, 2019). Similarly, DHEA has a well-established diurnal rhythm, with a post-awakening burst followed by a steady decline throughout the day, flattening between 6 and 9 h after waking (Heaney et al., 2012; Hucklebridge et al., 2005). As Himba women typically wake around 6AM (Prall et al., 2018), this sampling period also corresponds with a nadir in DHEA. Due to the narrow time window, inclusion of time of saliva collection had no impact on hormone predictions, and so is not included in this analysis. To account for within-subject variability, we attempted to collect up to three samples from each participant on non-consecutive days. As some women were not available for repeated sampling, or left the study area during sampling, number of samples varies by individual. We collected an average of 2.65 samples per women, although two women were only available for one sample (see Table 1). Saliva collections and other procedures took

Table 1 Participant characteristics

Variable	Mean	SD	Min	Max
Age	33.1	12.3	18	66
BMI*	25.1	3.0	17.5	30.4
N Children	4	2.8	0	10
N Saliva Samples	2.65	0.57	1	3

^{*}All Himba women wear a number of traditional items, including heavy anklets, leather skirts, and hair mixed with otjize (butterfat and ochre pigment) all which cannot be removed for weighing. As a result, we estimate that weight measurements are inflated by several kg, which will increase BMI estimates



place in private, typically at the participant's household. Samples were immediately placed on ice, and frozen within 2–3 h of collection in a portable freezer. Saliva was not collected from participants who had recently eaten and, to avoid any contamination, participants were instructed to wash out their mouths with provided bottled water prior to sample collection (Gildner, 2021). Samples were shipped on ice to the Trumble Lab at Arizona State University, where they were stored at -80°C for 12 months prior to analysis. Salimetrics enzyme immunoassay kits were used to assess DHEA and testosterone concentrations on the second freeze—thaw (samples thawed once during shipping), according to manufacturer's instructions (Salimetrics #1-1202 and #1-2402). Intra-assay and inter-assay coefficients of variation for DHEA and testosterone were 5.2%, 4.2% and 4.4%, 3.6% respectively, and control values were within the recommended range. For two participants, one sample each had inadequate volume to assay both hormones, so only testosterone is available, resulting in 122 samples for testosterone and 120 samples for DHEA.

Stress Survey

A focus group was held with Himba women to determine the range of stressors they experience. Responses from this focus group were used to develop a short eight question stress survey (see Fig. 1), which all participants completed. Three domains were included: resource, health, and social stressors. Women were asked how frequently over the last thirty days they worried each stressor using a Likert scale response of never/sometimes/often. Some participants were not married and/or did not have children, so they were not asked questions about these stressors. To maximize the sample size available, we used a subset of the questions in the full model (removing Q2 and Q7, as not all women in our sample were currently married and/or had children), as to allow comparison of all women who collected saliva for hormone analysis. Survey reliability was assessed via Cronbach's α from the ltm package (Rizopoulos, 2006). Summary scores were computed from stress survey responses. Since stress responses were strongly

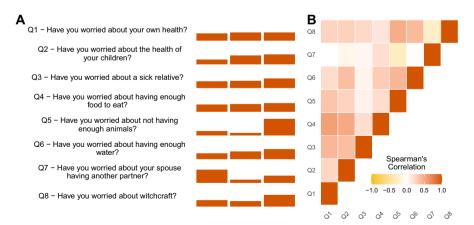


Fig. 1 Stress survey description. A Individual questions and the frequency of their responses (never, sometimes, often, from left to right); B Correlation matrix of question responses



associated with age, we calculated age-corrected residuals for standardized stress summary scores using a simple polynomial (age²). These age-corrected residuals were then used to predict androgens. Next, to better understand how different types of stressors impact androgens, we separated questions into the three domains: health stressors (Q1, Q2, Q3), resource stressors (Q4, Q5, Q6), and social stressors (Q7 and Q8). We summarized responses and calculated age-corrected residuals and then modeled the impact of these stressor types individually as shown below.

Analysis

DHEA and testosterone were jointly predicted in a multivariate model, with varying intercepts by individual (α_{ID}) to correct for repeated measurement. As we know these hormone levels are related, the model assumes correlated varying effects by individual (ρ) . We anticipated age to have a non-linear relationship with hormone concentrations, so age was modeled using a spline via the s() function in the brms package, defined as $\sum W_k A_k$ below. The model uses a log-normal distribution, and also includes a distributional component for both DHEA and testosterone outcomes shown below.

$$\begin{array}{l} {}^{DHEA}_{Testosterone} \sim \alpha + \alpha_{ID} + \sum W_k A_k + BMI * \beta_{BMI} + Stress * \beta_S \\ {}^{\delta_{DHEA}}_{\delta_{Testosterone}} \sim \alpha + Age * \beta_{Age} + Stress * \beta_S \end{array}$$

Prior selection was based on expectations of standard hormone levels as provided by assay manufacturers, as well as prior literature. To predict DHEA, we assume a negative effect of stress based on previously published work and chose a weak regularizing prior of normal (-1,1), while the effect of energy balance (BMI) receives a prior of normal (1,1). All other predictors received a regularized prior of normal (0,1), and variance components using exponential (1). Testing variations of priors, including default student-t priors, had little effect on results. Where relevant we report the proportion of the posterior distribution above or below zero (pr[b] > / < 0), or 95% prediction intervals (95% PI). All models were run in R version 4.3.0 (R Core Team, 2023), and were fitted to Rstan using the brms package (Bürkner, 2017; Stan Development Team, 2019). Models were run in three chains of 4000 iterations per chain, half warmup, and convergence assessed using the Gelman-Rubin convergence diagnostic ($\hat{R} = 1$ for all model parameters). Additional packages used for data cleaning and visualization include tidyverse, janitor, tidybayes, modelr, lubridate, broom, cowplot, patchwork, and ggthemr (Firke, 2021; Grolemund & Wickham, 2011; Kay, 2020; Pedersen, 2022; Robinson & Hayes, 2023; Tobin, 2020; Wickham, 2019, 2023; Wilke, 2017).

Results

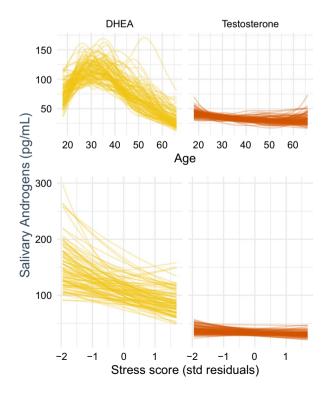
A total of 127 women completed the stress survey (of which a subset also provided hormones), and these data were used to calculate age-corrected standardized residuals. Of women who completed both the stress survey and hormone sampling, worries about livestock showed the most frequent number of "always" responses, while



worries over infidelity were least likely to be reported as a frequent worry (see also Prall & Scelza, 2023). Standardized Cronbach's α was estimated at 0.772 (95% CI=0.619 to 0.792, N=126) for the items used in this analysis, and 0.692 (95% CI=0.576 to 0.768, N=102) for all items in the stress survey. Figure 1 illustrates the frequency of each response type by question, and Spearman's correlations for all question responses in this study.

DHEA and testosterone samples were strongly positively correlated (Pearson's r=0.42). In the model, varying intercepts by individual for each hormone outcome were also positively correlated ($\rho = 0.82, 95\%$ PI=0.58 to 0.98), indicating that women who have high DHEA also tend to have high testosterone. The main statistical model includes a unique age spline for both DHEA and testosterone (Fig. 2). As in other populations, age predictions for DHEA show an increase in concentrations until around age thirty, followed by a lifelong decline. In this case, DHEA concentrations reach their model estimated peak between 33 and 34 years, before beginning a steady decline. This model estimates that women at 60 have 37% of the DHEA levels they had at their peak levels of age 34. Testosterone concentrations were relatively flat across the life course, with women at 18 having the highest testosterone, and concentrations showing only a slight decline with advanced age so that women at 60 have 75% of the testosterone concentrations of a woman of 18. Standardized BMI predicted increased DHEA ($\beta_{RMI} = 0.23$, 95% CI=0.03 to 0.43, pr[b]>0=98.6%), but only weakly predicted testosterone concentrations (β_{BMI} = 0.10, 95% CI = -0.05 to 0.24, pr[b] > 0 = 90.6%). Age and stress scores had minimal

Fig. 2 Posterior predictions of the main model. Each line represents one of one hundred draws from the posterior. Top plots show the effect of age. Bottom plots show the effects of stress score residuals. DHEA predictions are on the left, and testosterone predictions are on the right



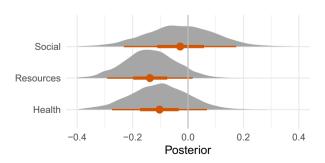


effect in predicting variance in DHEA ($\beta_{age} = 0.09$, 95% CI=-0.14 to 0.36, $\beta_S = 0.11$, 95% CI=-0.04 to 0.26) or testosterone ($\beta_{age} = 0.0$, 95% CI=-0.27 to 0.27, $\beta_S = -0.12$, 95% CI=-0.30 to 0.07). In the main model, age-corrected stress summary scores weakly and negatively predict DHEA ($\beta_S = -0.16$, 95% CI=-0.36 to 0.03, pr[b]<0=95.1%), but not testosterone ($\beta_S = -0.04$, 95% CI=-0.19 to 0.10, pr[b]<0=70%). Models comparing stress domains to hormone outcomes suggest that resource stressors are most strongly associated with relatively lower DHEA concentrations (pr[b]<0=92.4%), followed by health stressors (pr[b]<0=85.3%), while social stressors alone have little impact (pr[b]<0=60.2%, see Fig. 3). As with the summary score, stress domains had little impact on testosterone.

Discussion

Past work examining the interactions between stress and endocrine physiology highlight the responsiveness of adrenal androgens to acute and chronic stress. In industrialized populations, chronic stress is typically associated with a reduction in DHEA/S (Lennartsson et al., 2022, 2013a, b). In accordance with previous studies, we find a weak negative effect of reported stressors in the past thirty days with concentrations of salivary DHEA in this sample of women from a resource-limited subsistence-based population. Notably, DHEA, but not physiologically related and highly correlated testosterone, was responsive to perceived stressors. In examining the type of stressors most strongly associated with adrenal androgen reduction, questions related to resources had the largest impact. Himba women may be particularly sensitive to resource shortfalls as preparing food and monitoring stores for the household falls on their shoulders. Additionally, resource stress is at the root of other types of stressors, including those related to child health, pregnancy and lactation. The Kunene region has recently experienced a decade long drought, putting further strain on women's access to resources and coping strategies (Bollig, 2023; Hazel et al., 2021; Inman et al., 2020; Prall & Scelza, 2023). These ecological forces may predispose women to be more sensitive to resource related stressors. Importantly, by looking for relationships between endocrine physiology and different domains of stressors we demonstrate the importance of looking for stress responses that are ecologically relevant.

Fig. 3 Effect of stressor domain on DHEA outcomes. Each distribution represents the posterior distribution of the standardized residual of the stressor score





Our results also indicate the similarity in age-related DHEA profiles across populations. DHEA has a very specific curvilinear age pattern in adults, peaking in the late 20s and early 30s, before a lifelong decline (Labrie et al., 1997; Nafziger et al., 1998; Orentreich et al., 1984; Šulcová et al., 1997). Differences in the timing of maturational events leading to DHEA/S synthesis have been examined across populations, implicating differences in the timing related to ecology and stress (Helfrecht et al., 2018, 2023). However, few studies examine age profiles in non-industrialized populations. Bolivian women showed a similar peak, with DHEA at its highest in the third decade of life (Gonzales et al., 2002). Significant differences were found between women at sea level and at high altitude, where high altitude women showed a later peak in DHEA-S, faster declines with age, and lower hormone concentrations overall. Campbell et al. (2007) examined DHEA/S in Turkana men from blood samples showed a similar curvilinear shape, and found that DHEA/S didn't peak until the 30s and 40s, with differences between settled and nomadic men. Population distinctions in age profiles are difficult to assess given differences in measurement and assay types, but the curvilinear pattern seems robust, in contrast with population differences in testosterone (Ellison, 2002). Our results largely correspond to existing studies, with peak DHEA concentrations at 33 to 34 years of age in Himba women.

Unlike DHEA, testosterone was not associated with perceived stress, and showed only modest declines with age. Studies in industrialized populations report strong declines in female testosterone with age (Davison et al., 2005). Previous studies have shown minimal and contradictory impacts of various types stressors on women's testosterone levels. Women's testosterone is equally of adrenal and ovarian origin (Longcope, 1986), so changes in synthesis via the HPA axis only partially encompasses the physiological pathway that may influence concentrations. As such, women's testosterone levels may be less responsive to HPA activity. Other studies have found that women's testosterone may be responsive to motherhood (Barrett et al., 2013), but our sample consisted mostly of women with at least one child, so we are not able to test this prediction. Future work should focus on disentangling the social and psychological pathways that alter or disrupt women's androgen production, and include both testosterone and DHEA as relevant hormones implicated in women's health and behavior.

Our study has several notable limitations. We focus on DHEA here, as the active form of the hormone, but other studies measure only DHEA-S, complicating the potential to compare results. Our sample size is relatively small, making assessment of small effect sizes difficult. Given the population in question, we were unable to account for variation in reproductive parameters such as cycle effects. The design of this study is cross-sectional, making it impossible to examine within-person effects of chronic stressors on basal androgens. However, our main finding, that chronic stressors can negatively impact DHEA concentration has been found in several different populations under different contexts. The stress survey utilized here, derived from focus groups with women, is highly culturally specific. This has the benefit of actively addressing the causes of stress that Himba women report as stressful. However, the survey we developed has few questions about interpersonal social stressors, uncontrollable, or socially evaluative tasks, which other research highlights as important in HPA activity



(Dickerson & Kemeny, 2004). As such, the design of our survey is somewhat limited for interpreting which aspects of psychological stress most alter androgen production.

Overall results of this study highlight the association of basal adrenal androgen production to social and ecological stress in a non-industrialized, subsistence-based population. As with previous studies conducted in industrialized countries, reduced DHEA is associated with chronic stress. Potential alterations in adrenal androgen concentrations are non-trivial. DHEA/S is implicated in a number of health related outcomes, including cardiovascular disease (Mannella et al., 2018), obesity (Aoki & Terauchi, 2018), cancer (Labrie et al., 2003), as well as a number of behaviors and syndromes (Peixoto et al., 2017; Urbanski, 2021; Wolkowitz et al., 1997). These potential relationships can be convoluted, with opposing effects depending on concentration, individual characteristics, timeframe, and physiological system. DHEA/S has also been implicated in healthy aging, and use of pharmaceutical DHEA has been successfully applied to a number of conditions (Klinge et al., 2018; Labrie, 2010). DHEA/S levels have been associated with immune function, parasitism, and response to vaccination (Prall & Muehlenbein, 2018). These numerous associations are complex, and researchers continue to have difficulty disassociating low DHEA and negative health outcomes from confounding physiological interactions which may indirectly lower DHEA. Nevertheless, variation in adrenal androgen concentrations meaningfully associate with health outcomes, so understanding drivers of DHEA variation remains crucial to linking health disparities with chronic stressors.

Acknowledgements We would like to thank the community of Omuhonga for continued support and the individuals who participated in the study. J. Jakurama, G. Louis, and C. Louis acted as research assistants and translators in Namibia.

Author contributions S.P. and B.S. conducted the fieldwork and collected samples, and S.P. and B.T. conducted the laboratory analyses. S.P. analyzed the data, and wrote the manuscript with assistance from B.S. and B.T.

Funding This work was funded by the National Science Foundation BCS-1534682 awarded to BS.

Data Availability The data generated and analyzed during the current study are available on OSF at https://osf.io/p8b6u/.

Declarations

Ethical Approval Human subject permissions were issued by the UCLA Office of the Human Research Protection Program.

Competing Interests The authors declare no competing interests.

References

Aoki, K., & Terauchi, Y. (2018). Effect of Dehydroepiandrosterone (DHEA) on diabetes mellitus and obesity. In *Vitamins and Hormones* (Vol. 108, pp. 355–365). Elsevier. https://doi.org/10.1016/bs.vh. 2018.01.008



- Arnetz, J., Sudan, S., Goetz, C., Counts, S., & Arnetz, B. (2019). Nurse work environment and stress biomarkers: Possible implications for patient outcomes. *Journal of Occupational and Environmental Medicine*, 61(8), 676. https://doi.org/10.1097/JOM.000000000001642
- Barrett, E. S., Tran, V., Thurston, S., Jasienska, G., Furberg, A.-S., Ellison, P. T., & Thune, I. (2013). Marriage and motherhood are associated with lower testosterone concentrations in women. *Hormones and Behavior*, 63(1), 72–79. https://doi.org/10.1016/j.yhbeh.2012.10.012
- Bauer, M. E., Jeckel, C. M. M., & Luz, C. (2009). The role of stress factors during aging of the immune system. *Annals of the New York Academy of Sciences*, 1153(1), 139–152. https://doi.org/10.1111/j. 1749-6632.2008.03966.x
- Bollig, M. (1998). The colonial encapsulation of the north-western Namibian pastoral economy. *Africa*, 68(4), 506–536.
- Bollig, M. (2006). Risk management in a hazardous environment: A comparative study of two pastoral societies. Springer US. https://doi.org/10.1007/978-0-387-27582-6
- Bollig, M. (2023). Drought, disaster, and identity in north-western Namibia in times of global climate change. In *Climate change epistemologies in Southern Africa* (1st ed., pp. 27–48). Routledge. https://doi.org/10.4324/9781003180814-3
- Brzoza, Z., Kasperska-Zajac, A., Badura-Brzoza, K., Matysiakiewicz, J., Hese, R. T., & Rogala, B. (2008). Decline in dehydroepiandrosterone sulfate observed in chronic Urticaria is associated with psychological distress. *Psychosomatic Medicine*, 70(6), 723–728. https://doi.org/10.1097/PSY. 0b013e31817bcc8d
- Bürkner, P.-C. (2017). brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software*, 80(1), 1–28. https://doi.org/10.18637/jss.v080.i01
- Campbell, B. C., Leslie, P., & Campbell, K. (2007). Age-related patterns of DHEAS among Turkana males of northern Kenya. *The Aging Male, 10*(4), 203–209. https://doi.org/10.1080/1368553070 1533151
- Cardounel, A., Regelson, W., & Kalimi, M. (1999). Dehydroepiandrosterone protects hippocampal neurons against neurotoxin-induced cell death: Mechanism of Action2. Proceedings of the Society for Experimental Biology and Medicine, 222(2), 145–149.
- Chichinadze, K., & Chichinadze, N. (2008). Stress-induced increase of testosterone: Contributions of social status and sympathetic reactivity. *Physiology & Behavior*, 94(4), 595–603. https://doi.org/10.1016/j.physbeh.2008.03.020
- Clark, B. J., Prough, R. A., & Klinge, C. M. (2018). Mechanisms of action of dehydroepiandrosterone. In Vitamins and hormones (Vol. 108, pp. 29–73). Elsevier. https://doi.org/10.1016/bs.vh.2018.02.003
- Daly, W., Seegers, C. A., Rubin, D. A., Dobridge, J. D., & Hackney, A. C. (2005). Relationship between stress hormones and testosterone with prolonged endurance exercise. *European Journal of Applied Physiology*, 93(4), 375–380. https://doi.org/10.1007/s00421-004-1223-1
- Davison, S. L., Bell, R., Donath, S., Montalto, J. G., & Davis, S. R. (2005). Androgen levels in adult females: Changes with age, menopause, and oophorectomy. *The Journal of Clinical Endocrinology* & *Metabolism*, 90(7), 3847–3853. https://doi.org/10.1210/jc.2005-0212
- Dickerson, S. S., & Kemeny, M. E. (2004). Acute stressors and cortisol responses: A theoretical integration and synthesis of laboratory research. *Psychological Bulletin*, 130(3), 355.
- Dutheil, F., de Saint Vincent, S., Pereira, B., Schmidt, J., Moustafa, F., Charkhabi, M., et al. (2021).
 DHEA as a biomarker of stress: A systematic review and meta-analysis. Frontiers in Psychiatry, 12, 688367. https://doi.org/10.3389/fpsyt.2021.688367
- Edwards, D. A., & Casto, K. V. (2015). Baseline cortisol moderates testosterone reactivity to women's intercollegiate athletic competition. *Physiology & Behavior*, *142*, 48–51. https://doi.org/10.1016/j.physbeh.2015.01.037
- Ellison, P. T. (2002). Population variation in age-related decline in male salivary testosterone. *Human Reproduction*, 17(12), 3251–3253. https://doi.org/10.1093/humrep/17.12.3251
- Firke, S. (2021). Janitor: Simple tools for examining and cleaning dirty data (version 2.2). https:// CRAN.R-project.org/package=janitor
- Gallagher, S., Sumner, R. C., Muldoon, O. T., Creaven, A.-M., & Hannigan, A. (2016). Unemployment is associated with lower cortisol awakening and blunted dehydroepiandrosterone responses. *Psycho-neuroendocrinology*, 69, 41–49. https://doi.org/10.1016/j.psyneuen.2016.03.011
- Gettler, L. T., McDade, T. W., Feranil, A. B., Agustin, S. S., & Kuzawa, C. W. (2014). Salivary estradiol and testosterone in filipino men: Diurnal patterns and relationships with adiposity: Male E2 and Adiposity. American Journal of Human Biology, 26(3), 376–383. https://doi.org/10.1002/ajhb. 22528



- Gettler, L. T., Sarma, M. S., Lew-Levy, S., Bond, A., Trumble, B. C., & Boyette, A. H. (2019). Mothers' and fathers' joint profiles for testosterone and oxytocin in a small-scale fishing-farming community: Variation based on marital conflict and paternal contributions. *Brain and Behavior*, 9(9). https://doi.org/10.1002/brb3.1367
- Gildner, T. E. (2021). Reproductive hormone measurement from minimally invasive sample types: Methodological considerations and anthropological importance. *American Journal of Human Biology*, 33(1). https://doi.org/10.1002/ajhb.23535
- Goldey, K. L., & Van Anders, S. M. (2015). Sexual modulation of testosterone: Insights for humans from across species. Adaptive Human Behavior and Physiology, 1(2), 93–123. https://doi.org/10.1007/ s40750-014-0005-1
- Gonzales, G., Gonez, C., & Villena, A. (2002). Adrenopause or decline of serum adrenal androgens with age in women living at sea level or at high altitude. *Journal of Endocrinology*, 173(1), 95–101. https://doi.org/10.1677/joe.0.1730095
- Grolemund, G., & Wickham, H. (2011). Dates and times made easy with {lubridate}. *Journal of Statistical Software*, 40(3), 1–25.
- Handelsman, D. J., Hirschberg, A. L., & Bermon, S. (2018). Circulating testosterone as the hormonal basis of sex differences in athletic performance. *Endocrine Reviews*, 39(5), 803–829. https://doi.org/ 10.1210/er.2018-00020
- Hazel, A., Meeks, G., Bharti, N., Jakurama, J., Matundu, J., & Jones, J. H. (2021). Opportunities and constraints in women's resource security amid climate change: A case study of arid-living Namibian agro-pastoralists. *American Journal of Human Biology*, 33(4), e23633. https://doi.org/10.1002/ajhb. 23633
- Hazeldine, J., Arlt, W., & Lord, J. M. (2010). Dehydroepiandrosterone as a regulator of immune cell function. The Journal of Steroid Biochemistry and Molecular Biology, 120(2–3), 127–136.
- Heaney, J. L. J., Phillips, A. C., & Carroll, D. (2012). Ageing, physical function, and the diurnal rhythms of cortisol and dehydroepiandrosterone. *Psychoneuroendocrinology*, *37*(3), 341–349. https://doi.org/10.1016/j.psyneuen.2011.07.001
- Helfrecht, C., Hagen, E. H., DeAvila, D., Bernstein, R. M., Dira, S. J., & Meehan, C. L. (2018). DHEAS patterning across childhood in three sub-Saharan populations: Associations with age, sex, ethnicity, and cortisol. *American Journal of Human Biology*, 30(2), e23090.
- Helfrecht, C., Wang, H., Dira, S. J., DeAvila, D., & Meehan, C. L. (2023). DHEAS and nutritional status among Sidama, Ngandu, and Aka children: Effects of cortisol and implications for adrenarche. *American Journal of Human Biology*, *35*(7), e23881. https://doi.org/10.1002/ajhb.23881
- Hermans, E. J., Putman, P., Baas, J. M., Gecks, N. M., Kenemans, J. L., & Van Honk, J. (2007). Exogenous testosterone attenuates the integrated central stress response in healthy young women. *Psychoneuroendocrinology*, 32(8–10), 1052–1061. https://doi.org/10.1016/j.psyneuen.2007.08.006
- Hucklebridge, F., Hussain, T., Evans, P., & Clow, A. (2005). The diurnal patterns of the adrenal steroids cortisol and dehydroepiandrosterone (DHEA) in relation to awakening. *Psychoneuroendocrinology*, 30(1), 51–57. https://doi.org/10.1016/j.psyneuen.2004.04.007
- Inman, E. N., Hobbs, R. J., & Tsvuura, Z. (2020). No safety net in the face of climate change: The case of pastoralists in Kunene Region, Namibia. PLOS ONE, 15(9), e0238982. https://doi.org/10.1371/ journal.pone.0238982
- Izawa, S., Sugaya, N., Shirotsuki, K., Yamada, K. C., Ogawa, N., Ouchi, Y., et al. (2008). Salivary dehydroepiandrosterone secretion in response to acute psychosocial stress and its correlations with biological and psychological changes. *Biological Psychology*, 79(3), 294–298.
- Jeckel, C. M. M., Lopes, R. P., Berleze, M. C., Luz, C., Feix, L., de Lima Argimon, I. I., et al. (2010). Neuroendocrine and immunological correlates of chronic stress in 'Strictly Healthy' populations. *Neuroimmunomodulation*, 17(1), 9–18. https://doi.org/10.1159/000243080
- Joseph, J. J., & Golden, S. H. (2017). Cortisol dysregulation: The bidirectional link between stress, depression, and type 2 diabetes mellitus. Annals of the New York Academy of Sciences, 1391(1), 20–34. https://doi.org/10.1111/nyas.13217
- Juster, R.-P., McEwen, B. S., & Lupien, S. J. (2010). Allostatic load biomarkers of chronic stress and impact on health and cognition. *Neuroscience & Biobehavioral Reviews*, 35(1), 2–16. https://doi. org/10.1016/j.neubiorev.2009.10.002
- Karishma, K. K., & Herbert, J. (2002). Dehydroepiandrosterone (DHEA) stimulates neurogenesis in the hippocampus of the rat, promotes survival of newly formed neurons and prevents corticosteroneinduced suppression. *European Journal of Neuroscience*, 16(3), 445–453. https://doi.org/10.1046/j. 1460-9568.2002.02099.x



- Kay, M. (2020). tidybayes: Tidy Data and Geoms for Bayesian Models. https://doi.org/10.5281/zenodo. 1308151
- Kimonides, V. G., Spillantini, M. G., Sofroniew, M. V., Fawcett, J. W., & Herbert, J. (1999). Dehydroe-piandrosterone antagonizes the neurotoxic effects of corticosterone and translocation of stress-activated protein kinase 3 in hippocampal primary cultures. *Neuroscience*, 89(2), 429–436.
- Klinge, C. M., Clark, B. J., & Prough, R. A. (2018). Dehydroepiandrosterone research: Past, current, and future. In *Vitamins and hormones* (Vol. 108, pp. 1–28). Elsevier. https://doi.org/10.1016/bs.vh.2018. 02.002
- Kreuz, M. L. E. (1972). Suppression of plasma testosterone levels and psychological stress: A longitudinal study of young men in officer candidate school. Archives of General Psychiatry, 26(5), 479. https://doi.org/10.1001/archpsyc.1972.01750230089017
- Labrie, F., Langer, A. B., Cusan, L., & Candas, B. (1997). Marked decline in serum concentrations of adrenal C19 sex steroid precursors and conjugated androgen metabolites during aging. *The Journal of Clinical Endocrinology & Metabolism*, 82(8), 2396–2402.
- Labrie, F., Luu-The, V., Labrie, C., Bélanger, A., Simard, J., Lin, S.-X., & Pelletier, G. (2003). Endocrine and intracrine sources of androgens in women: Inhibition of breast cancer and other roles of androgens and their precursor dehydroepiandrosterone. *Endocrine Reviews*, 24(2), 152–182.
- Labrie, F., Martel, C., & Balser, J. (2011). Wide distribution of the serum dehydroepiandrosterone and sex steroid levels in postmenopausal women: Role of the ovary? *Menopause*, 18(1), 30. https://doi.org/10.1097/gme.0b013e3181e195a6
- Labrie, F. (2010). DHEA, important source of sex steroids in men and even more in women. In *Progress in brain research* (Vol. 182, pp. 97–148). Elsevier. https://doi.org/10.1016/S0079-6123(10)82004-7
- Lac, G., Dutheil, F., Brousse, G., Triboulet-Kelly, C., & Chamoux, A. (2012). Saliva DHEAS changes in patients suffering from psychopathological disorders arising from bullying at work. *Brain and Cognition*, 80(2), 277–281.
- Lennartsson, A.-K., Kushnir, M. M., Bergquist, J., Billig, H., & Jonsdottir, I. H. (2012). Sex steroid levels temporarily increase in response to acute psychosocial stress in healthy men and women. *International Journal of Psychophysiology*, 84(3), 246–253. https://doi.org/10.1016/j.ijpsycho.2012.03.001
- Lennartsson, A.-K., Theorell, T., Kushnir, M. M., Bergquist, J., & Jonsdottir, I. H. (2013a). Perceived stress at work is associated with attenuated DHEA-S response during acute psychosocial stress. *Psychoneuroendocrinology*, *38*(9), 1650–1657. https://doi.org/10.1016/j.psyneuen.2013.01.010
- Lennartsson, A.-K., Theorell, T., Rockwood, A. L., Kushnir, M. M., & Jonsdottir, I. H. (2013b). Perceived stress at work is associated with lower levels of DHEA-S. *PLoS ONE*, 8(8), e72460. https://doi.org/10.1371/journal.pone.0072460
- Lennartsson, A.-K., Arvidson, E., Börjesson, M., & Jonsdottir, I. H. (2022). DHEA-S production capacity in relation to perceived prolonged stress. Stress, 25(1), 105–112. https://doi.org/10.1080/10253890.2021.2024803
- Longcope, C. (1986). Adrenal and gonadal androgen secretion in normal females. Clinics in Endocrinology and Metabolism, 15(2), 213–228.
- Lupien, S., Lecours, A., Lussier, I., Schwartz, G., Nair, N., & Meaney, M. (1994). Basal cortisol levels and cognitive deficits in human aging. *The Journal of Neuroscience*, 14(5), 2893–2903. https://doi. org/10.1523/JNEUROSCI.14-05-02893.1994
- Mannella, P., Simoncini, T., Caretto, M., & Genazzani, A. R. (2018). Dehydroepiandrosterone and cardiovascular disease. In *Vitamins and hormones* (Vol. 108, pp. 333–353). Elsevier. https://doi.org/10.1016/bs.yh.2018.05.001
- Markopoulou, K., Papadopoulos, A., Juruena, M. F., Poon, L., Pariante, C. M., & Cleare, A. J. (2009). The ratio of cortisol/DHEA in treatment resistant depression. *Psychoneuroendocrinology*, 34(1), 19–26
- Mason, J., Tolson, W., Robinson, J., Brady, J., Tolliver, G., & Johnson, T. (1968). Urinary androsterone, etiocholanolone, and dehydroepiandrosterone responses to 72-hr. avoidance sessions in the monkey. *Psychosomatic Medicine*, 30(5), 710–720.
- McEwen, B. S. (2007). Physiology and neurobiology of stress and adaptation: Central role of the brain. *Physiological Reviews*, 87(3), 873–904. https://doi.org/10.1152/physrev.00041.2006
- McEwen, B. S., & Stellar, E. (1993). Stress and the individual: Mechanisms leading to disease. *Archives of Internal Medicine*, 153(18), 2093–2101.
- Nafziger, A. N., Bowlin, S. J., Jenkins, P. L., & Pearson, T. A. (1998). Longitudinal changes in dehydroepiandrosterone concentrations in men and women. *Journal of Laboratory and Clinical Medicine*, 131(4), 316–323.



- NHDR. (2019). UNDP Namibia Annual Report 2019.
- Orentreich, N., Brind, J. L., Rizer, R. L., & Vogelman, J. H. (1984). Age changes and sex differences in serum dehydroepiandrosterone sulfate concentrations throughout adulthood. *The Journal of Clinical Endocrinology & Metabolism*, 59(3), 551–555. https://doi.org/10.1210/jcem-59-3-551
- Pedersen, T. L. (2022). patchwork: The Composer of Plots (version 1.1.2). https://CRAN.R-project.org/package=patchwork
- Peixoto, C., Carrilho, C. G., Barros, J. A., Ribeiro, T., Silva, L. M., Nardi, A. E., et al. (2017). The effects of dehydroepiandrosterone on sexual function: A systematic review. *Climacteric*, 20(2), 129–137.
- Phillips, A. C., Carroll, D., Gale, C. R., Lord, J. M., Arlt, W., & Batty, G. D. (2010). Cortisol, DHEA sulphate, their ratio, and all-cause and cause-specific mortality in the Vietnam Experience Study. *European Journal of Endocrinology*, 163(2), 285–292.
- Pluchino, N., Drakopoulos, P., Bianchi-Demicheli, F., Wenger, J. M., Petignat, P., & Genazzani, A. R. (2015). Neurobiology of DHEA and effects on sexuality, mood and cognition. *The Journal of Steroid Biochemistry and Molecular Biology*, 145, 273–280. https://doi.org/10.1016/j.jsbmb.2014.04.012
- Powell, L. H., Lovallo, W. R., Matthews, K. A., Meyer, P., Midgley, A. R., Baum, A., et al. (2002). Physiologic markers of chronic stress in premenopausal middle-aged women. *Psychosomatic Medicine*, 64(3), 502–509. https://doi.org/10.1097/00006842-200205000-00015
- Prall, S. P., & Scelza, B. A. (2020a). Why men invest in non-biological offspring: Paternal care and paternity confidence among Himba pastoralists. *Proceedings of the Royal Society B: Biological Sciences*, 287(1922), 20192890. https://doi.org/10.1098/rspb.2019.2890
- Prall, S. P., & Scelza, B. A. (2020b). Resource demands reduce partner discrimination in Himba women. *Evolutionary Human Sciences*, 2, e45. https://doi.org/10.1017/ehs.2020.43
- Prall, S. P., & Scelza, B. A. (2023). The dietary impacts of drought in a traditional pastoralist economy. American Journal of Human Biology, 35(1), e23803. https://doi.org/10.1002/ajhb.23803
- Prall, S. P., Larson, E. E., & Muehlenbein, M. P. (2017). The role of dehydroepiandrosterone on functional innate immune responses to acute stress. *Stress and Health*, 33(5), 656–664.
- Prall, S. P., Yetish, G., Scelza, B. A., & Siegel, J. M. (2018). The influence of age- and sex-specific labor demands on sleep in Namibian agropastoralists. Sleep Health, 4(6), 500–508. https://doi.org/ 10.1016/j.sleh.2018.09.012
- Prall, S. P., & Muehlenbein, M. P. (2018). DHEA modulates immune function: A review of evidence. In Vitamins and hormones (Vol. 108, pp. 125–144). Elsevier. https://doi.org/10.1016/bs.vh.2018.01. 023
- Quinn, T., Greaves, R., Badoer, E., & Walker, D. (2018). DHEA in prenatal and postnatal life: Implications for brain and behavior. In *Vitamins and hormones* (Vol. 108, pp. 145–174). Elsevier. https://doi.org/10.1016/bs.vh.2018.03.001
- R Core Team. (2023). R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/
- Rizopoulos, D. (2006). ltm: An R package for latent variable modelling and item response theory analyses. *Journal of Statistical Software*, 17(5), 1–25. https://doi.org/10.18637/jss.v017.i05
- Robinson, D., & Hayes, A. (2023). Broom: Convert statistical analysis objects into tidy tibbles (version 1.0.4). https://CRAN.R-project.org/package=broom
- Scelza, B. A., Prall, S. P., & Levine, N. E. (2019). The disequilibrium of double descent: Changing inheritance norms among Himba pastoralists. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 374(1780), 20180072. https://doi.org/10.1098/rstb.2018.0072
- Scelza, B. A., Prall, S. P., & Starkweather, K. (2020). Paternity confidence and social obligations explain men's allocations to romantic partners in an experimental giving game. *Evolution and Human Behavior*, 41(1), 96–103. https://doi.org/10.1016/j.evolhumbehav.2019.10.007
- Scelza, B. A., Prall, S. P., & Starkweather, K. (2021). The Role of Spousal Separation on Norms Related to Gender and Sexuality among Himba Pastoralists. *Social Sciences*, 10(5), 174. https://doi.org/10. 3390/socsci10050174
- Stan Development Team. (2023). RStan: the R interface to Stan (version 2.21.8). http://mc-stan.org/
- Šulcová, J., Hill, M., Hampl, R., & Starka, L. (1997). Age and sex related differences in serum levels of unconjugated dehydroepiandrosterone and its sulphate in normal subjects. *Journal of Endocrinol*ogy, 154(1), 57–62.
- Tobin, C. (2020). ggthemr: Themes for "ggplot2" (version 1.1). https://github.com/Mikata-Project/ggthemr



- Traish, A. M., Kang, H. P., Saad, F., & Guay, A. T. (2011). Dehydroepiandrosterone (DHEA)—A Precursor Steroid or an Active Hormone in Human Physiology (CME). *The Journal of Sexual Medicine*, 8(11), 2960–2982. https://doi.org/10.1111/j.1743-6109.2011.02523.x
- Trumble, B. C., Stieglitz, J., Jaeggi, A. V., Beheim, B., Schwartz, M., Seabright, E., et al. (2018). Parental hormones are associated with crop loss and family sickness following catastrophic flooding in low-land Bolivia. *Physiology & Behavior*, 193, 101–107. https://doi.org/10.1016/j.physbeh.2018.02.028
- Urbanski, H. F. (2021). DHEA as a biomarker of aging in humans and nonhuman primates: synthesis, neuroprotection, and cognitive function. In C.R. Martin, V.R. Preedy, & R. Rajendram (Eds.), Assessments, Treatments and Modeling in Aging and Neurological Disease (pp. 269–278). Academic Press.
- van Anders, S. M. (2013). Beyond masculinity: Testosterone, gender/sex, and human social behavior in a comparative context. *Frontiers in Neuroendocrinology*, 34(3), 198–210.
- Vingren, J. L., Kraemer, W. J., Ratamess, N. A., Anderson, J. M., Volek, J. S., & Maresh, C. M. (2010). Testosterone physiology in resistance exercise and training: The up-stream regulatory elements. *Sports Medicine*, 40(12), 1037–1053. https://doi.org/10.2165/11536910-0000000000-00000
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seidel, D.P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., & Yutani, H. (2019). Welcome to the tidyverse. *Journal of Open Source Software*, 4(43), 1686. https://doi.org/10.21105/joss.01686
- Wickham, H. (2023). modelr: Modelling Functions that Work with the Pipe (version 0.1.11). https:// CRAN.R-project.org/package=modelr
- Wilke, C. (2017). Cowplot: Streamlined Plot Theme and Plot Annotations for "ggplot2" (version 1.1.1). https://CRAN.R-project.org/package=cowplot
- Wingfield, J. C., & Sapolsky, R. M. (2003). Reproduction and resistance to stress: When and how: Reproduction and resistance to stress. *Journal of Neuroendocrinology*, 15(8), 711–724. https://doi.org/10.1046/j.1365-2826.2003.01033.x
- Wolkowitz, O. M., Reus, V. I., Roberts, E., Manfredi, F., Chan, T., Raum, W. J., et al. (1997). Dehydroe-piandrosterone (DHEA) treatment of depression. *Biological Psychiatry*, 41(3), 311–318. https://doi.org/10.1016/S0006-3223(96)00043-1

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.

