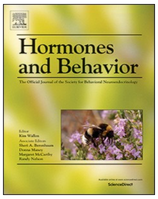
Hormones and Behavior 107 (2019) 35–45

Contents lists available at ScienceDirect

Hormones and Behavior

journal homepage: www.elsevier.com/locate/yhbeh



Testosterone, fathers as providers and caregivers, and child health: Evidence from fisher-farmers in the Republic of the Congo

Adam H. Boyette[a,*,1], Sheina Lew-Levy[b], Mallika S. Sarma[c], Lee T. Gettler[c,d,e,*,1]

[a] Thompson Writing Program, Duke University, Box 90025, Durham, NC 27708, USA
[b] Department of Psychology, University of Cambridge, Free School Lane CB2 3RQ, United Kingdom
[c] Department of Anthropology, University of Notre Dame, 244 Corbett Hall, Notre Dame, IN 46556, USA
[d] Eck Institute for Global Health, USA
[e] William J. Shaw Center for Children and Families, University of Notre Dame, 244 Corbett Hall, Notre Dame, IN 46556, USA

ARTICLE INFO

Keywords:
Androgens
Paternal care
Indirect care
Direct care
Child growth
Congo-Brazzaville
Subsistence agriculture

ABSTRACT

Males in vertebrate species with biparental care commonly face a life history trade-off between investing in mating versus parenting effort. Among these males, testosterone is frequently elevated during mating and competition and reduced when males help raise offspring. These physiological patterns may be adaptive, increasing males' fitness through investments in young. However, for some species, including humans, indirect parenting often benefits young but can also involve male competition and risk-taking behavior and may be facilitated by elevated testosterone. Despite potential adaptive functions of biological responses to invested fatherhood, few if any mammalian studies have linked fathers' testosterone to offspring outcomes; no studies in humans have. Using data from a small-scale society of fisher-farmers from the Republic of the Congo, we find that fathers who were rated as better providers by their peers had higher testosterone, compared to other fathers in their community. However, children whose fathers had middle-range T compared to fathers with higher or lower levels had better energetic status (higher BMI; greater triceps skinfold thickness). Fathers' indirect and direct care helped to account for these associations between paternal T and children's energetic profiles. Given that human paternal direct and, especially, indirect care are thought to have been important evolutionarily and remain so in many contemporary societies, these findings help to shed light on the facultative nature of human biological responses to fatherhood and the relevance of these factors to children's well-being.

ABSTRACT

Les mâles des espèces vertébrées où il existe des soins biparentaux sont souvent confrontés à faire des compromis entre l'investissement dans l'accouplement et les efforts parentaux. Parmi ces mâles, la testostérone est fréquemment élevée pendant l'accouplement et la compétition et plus réduite lorsque les hommes aident à élever leurs enfants. Ces patterns physiologiques peuvent être adaptatifs, ce qui augmente le succès reproducteur (fitness) des hommes grâce à un investissement dans leurs enfants. Cependant, pour certaines espèces, y compris les humains, la parentalité indirecte profite souvent aux enfants, mais peut également impliquer une compétition masculine et un comportement à risque, et peut-être facilitée par un taux élevé de testostérone. Malgré les fonctions adaptatives potentielles des réponses biologiques dans l'investissement paternel, presque aucune étude sur les mammifères n'a tenté d'établir un lien entre la testostérone des pères et la descendance (offspring outcomes) et c'est aussi le cas chez les humains. Les données collectées dans une micro-société des pêcheurs-fermiers de la République du Congo indiquent que les pères qui ont été évalués comme les meilleurs soutiens de famille de soins par leurs pairs avaient un taux de testostérone plus élevée que les autres pères de la communauté. Cependant, les enfants dont le père avait un taux situé dans la fourchette moyenne, comparativement aux pères avec des niveaux plus élevés ou plus faibles, avaient un meilleur statut énergétique (IMC plus élevé, épaisseur du pli cutané du triceps plus important). Les soins directs et indirects des pères ont contribué à

---

* Correspondence to: A.H. Boyette, Thompson Writing Program, Duke University, Box 90025, Durham, NC 27705, USA; L.T. Gettler, Department of Anthropology, University of Notre Dame, 244 Corbett Hall, Notre Dame, IN 46556, USA.

E-mail addresses: adam.boyette@duke.edu (A.H. Boyette), sheinalewlevy@gmail.com (S. Lew-Levy), Mallika.Sarma.1@nd.edu (M.S. Sarma), lgettler@nd.edu (L.T. Gettler).

[1] AHB and LTG contributed equally to this work.

https://doi.org/10.1016/j.yhbeh.2018.09.006
Received 6 April 2018; Received in revised form 15 August 2018; Accepted 25 September 2018

rendre compte des associations entre le profil paternel et le profil énergétique des enfants. Étant donné que les soins directs et, en particulier, les soins indirects paternels sont considérés comme importants d'un point évolutionnaire et qu'ils le demeurent dans de nombreuses sociétés contemporaines, ces résultats aident à comprendre le caractère facultatif des réponses biologiques humaines à la paternité et la pertinence de ces facteurs pour le bien-être des enfants.

1. Introduction

Among vertebrates, testosterone (T) plays an important physiological role in shaping male life history strategies. Elevated T often mediates life history trade-offs by influencing the allocation of limited time and energetic resources to reproduction over survival. In this role, T commonly mechanistically allocates resources towards mating-related somatic (e.g. musculature, ornamentation) and behavioral (e.g. competition, risk-taking) components of male reproductive effort (Bribiescas, 2001; Goymann et al., 2007; Gray et al., 2017; Hau, 2007; Muehlenbein and Bribiescas, 2005; Muller, 2017). For species in which biparental care has evolved, males face an additional reproductive-related trade-off between mating and parenting effort during periods in which offspring are dependent (Hirschenhauser and Oliveira, 2006; Wingfield et al., 1990). For such vertebrates, it is relatively common for males to have elevated T during the season or life history period in which they compete for mating opportunities, resources, and status and to exhibit reduced T when they partner with females, including to cooperate in parental care (Goymann et al., 2007; Hirschenhauser and Oliveira, 2006; Storey and Ziegler, 2016; Wingfield et al., 1990). This conceptual framework emerged from decades of bird behavioral and physiological data (Goymann et al., 2007; Wingfield et al., 1990). It is now seen as broadly applicable to species in multiple vertebrate taxa (Hirschenhauser and Oliveira, 2006; Storey et al., 2006) including mammals, among which biparental care is relatively rare (i.e. compared to birds and fish) and singular paternal care, as a species wide norm, is absent (Clutton-Brock, 1991; Gettler, 2014; Saltzman and Ziegler, 2014; Storey and Ziegler, 2016).

Humans are one such mammalian species to which this model appears to generally apply. In multiple, variable cultural and ecological settings it has been shown that fathers who participate in more direct care (Gettler, 2016a; Gray et al., 2017; Rilling, 2013; Storey and Ziegler, 2016; van Anders, 2013) and who sleep in close proximity to their families have lower T than do other fathers (Gettler et al., 2012; Lawson et al., 2017). Complementing the data on human paternal physiology and care and also consistent with the notion that social monogamy tends to evolutionarily precede paternal care among mammals (Lukas and Clutton-Brock, 2013), men in monogamous relationships tend to have reduced T compared to single males (Gettler, 2016a; Gray et al., 2017; van Anders et al., 2011; van Anders, 2013). Meanwhile, partnered men who report greater interest in extra-pair sexual and romantic opportunities or lower relationship commitment or investment maintain relatively elevated T (Edelstein et al., 2011; McIntyre et al., 2006; van Anders and Goldey, 2010).

Consistent with interpretations for similar patterns in other taxa (Hirschenhauser and Oliveira, 2006; Wingfield et al., 1990), these results are hypothesized to reflect selection for physiological mechanisms that help facilitate males' cooperation with females to raise highly dependent offspring (Gettler, 2016a; Gettler, 2014; Gettler, 2010; Gray et al., 2017; Storey and Ziegler, 2016). Because reduced paternal T helps facilitate parenting effort and focus males away from mating effort, it should tend to increase offspring survival and quality in species that have evolved biparental care. While there is support for this perspective in studies of some bird species (Reed et al., 2006), this link between fathers' T and offspring outcomes is largely unexplored among mammalian species (Bales and Saltzman, 2016; Rosenbaum and Gettler, 2018). Along those lines, this potential linkage between fathers' T and child outcomes has not been tested in humans, to our knowledge. Adding further complexity, recent results indicate that men whose T or androgen functionality is too low may be prone towards depression or reduced parenting effort (Gettler et al., 2017; Saxbe et al., 2017). These newer data thus raise the question of whether there may be an inverted U-shaped curve relating fathers' T to child outcomes, potentially accounted for by paternal care, with children benefitting most when fathers' have medium-range T.

In support of such a possibility, evidence suggests that lower T is not uniformly linked to greater investment by males, within or across species. For example, while the model linking reduced T to male investment in pairbonding and parenting effort has broad support across vertebrates, there are notable exceptions in multiple taxonomic groups (Lynn, 2008; van Anders et al., 2011). These divergences have been shown among rodents (Trainor and Marler, 2001), fish (Desjardins et al., 2008), and birds (Goymann et al., 2007; Lynn, 2008) and shed light on both evolutionary and proximate influences on T's physiological functions. In the context of the debate around whether men's mating effort is misconstrued as parenting effort (Hawkes et al., 2001; Hawkes and Bliege Bird, 2002), some such patterns are at least consistent with long-standing observations that mating and parenting effort are often not separable (Smuts and Gubernick, 1992). Specifically, certain forms of paternal care that involve competition (e.g. for territory or resources) may be facilitated by elevated T rather than reduced T (van Anders, 2013; van Anders et al., 2011).

Furthermore, in species in which paternal care has evolved but males' roles are primarily restricted to domains that overlap with mating effort or those that might be more effectively facilitated by the maintenance of elevated T (e.g. competitive and risk taking behaviors), one would predict that males would not exhibit reduced T during seasons or phases of pairbonding or parenting (Gettler et al., 2015; Gray et al., 2017; van Anders et al., 2011). Among species in which paternal care is not obligate and in which males flexibly adjust their caregiving effort between domains, such as shifting relative investments in indirect and direct care (Clutton-Brock, 1991; Gettler, 2010; Marlowe, 1999), it is likely that male reproductive physiology will have been selected for plasticity to respond to cues and demands of the proximate context (Goymann et al., 2007; Lynn, 2008; Wingfield et al., 1990). Reflecting the imperfection and compromises inherent in evolutionary processes, both of these scenarios set up conflicts between the range of demands of pairbonding and biparental care and paternal physiological profiles. Fathers with elevated T may be effective at acquiring resources or protecting young or territory, but also less effectual at cooperating with mothers, more mating-oriented, and less sensitive to offspring needs. Experimental avian models in which males' T is artificially elevated during periods in which they would typically participate in biparental care have shown that they (instead) compete against other males and pursue extra-pair mating opportunities, offering support for this framework (Ketterson et al., 1992; Reed et al., 2006).

In humans, there is substantial variation between- and within-ecologies and societies in the extent to which males perform care and the forms that care takes. Thus, humans represent a notable test case to model the within-species range of paternal physiology profiles expressed under variable ecological and familial demands. As described above, much past research on human paternal physiology has focused on the association between T and fathers' direct caregiving rather than forms of indirect paternal care, such as provisioning, to which men more often commit their time and energy cross-culturally (Gettler, 2016a; Gettler, 2014; Gray and Anderson, 2010; Gurven and Hill, 2009;

van Anders, 2013; van Anders et al., 2011). Given the energetic demands of raising multiple slow developing offspring concurrently, as is common in natural fertility populations, provisioning is hypothesized to have been critical for the evolution of human's life history strategy (Gray and Anderson, 2010; Gurven and Hill, 2009; Kaplan et al., 2000), and provisioning and familial resources have been linked to child health and energetic status in subsistence-level societies (Boyette et al., 2018; Winking and Koster, 2015). In such societies, where calories can be periodically limited and pathogen exposure is typically high, improved energetic status substantially influences children's ability to ward off infectious disease (McDade et al., 2008; Nandy et al., 2005). In recent work from the present study population, we have shown that children with poorer indicators of long-term energetic condition were more likely to exhibit physiological markers of acute infection (Boyette et al., 2018). Through these pathways, paternal indirect care can have significant impacts on children's health outcomes. Moreover, the effects of energy restriction during childhood may translate into effects on adult health, cognitive function, and economic productivity (Martorell et al., 2010).

Here, we help shed light on these prevailing questions by testing hypotheses related to paternal T among a small-scale community of Bondongo fisher-farmers in the Republic of the Congo (ROC). As described previously (Boyette et al., 2018) and in further detail below, within this cultural group fathers' indirect forms of parental care, particularly provisioning and resource acquisition, are highly valued and emphasized as central to what men contribute to families. Men do engage in direct paternal care in this setting, though average levels are relatively low in cross-cultural comparison (Hewlett and Macfarlan, 2010; Gray and Anderson, 2010), and such care is more important after early childhood (e.g. socialization; tending to older children when they are sick). As we characterize in the Methods, valued indirect paternal care behaviors in this community often involve risk taking and men acquire social status through their success in these activities. Thus, theoretically, higher T could facilitate these types of behaviors (Archer, 2006; Gray et al., 2017; van Anders, 2013). However, fathers with extremely elevated T might additionally pursue mating effort at a cost to parenting, family function, and child health. For example, our past work in this context points to sexual jealousy as a major source of marital conflict (Boyette et al., 2018). Thus, we test competing hypotheses relating paternal T to men's parenting effort. We first test whether fathers with medium-range T engage in greater indirect care related to acquisition of resources compared to fathers with relatively lower or higher T (i.e. an inverted U-shaped curve). As an alternative hypothesis, we also test whether fathers with higher T engage in greater indirect care (i.e. a linear relationship). Given the extensive prior work linking lower paternal T to greater direct care (Gettler, 2016a; Gray et al., 2017; van Anders, 2013), we also test a similar hypothesis among these Bondongo fathers. However, we predict that direct care will not be significantly linked to their T, given its relatively low frequency and reduced cultural salience (Boyette et al., 2018; Gettler, 2016a). Additionally, we test whether fathers with medium-range T will have children in better health and energetic condition than fathers with relatively lower or higher T (i.e. an inverted U-shaped curve) or whether paternal T-child health relationships are linear. Finally, we test whether fathers' care helps to account for relationships between T and children's energetic status.

2. Methods

2.1. Study population and ethnographic context

The current study is part of a larger biocultural project on fatherhood, family systems, and child development among Bondongo fisher-farmers and BaYaka foragers in northern ROC. Our analyses here focus on the former group, who are residents of a village along the Motaba River in the Likouala Province. It takes 3 to 6 days to reach the site by hired transport from Brazzaville, ROC's capital city. The village itself is accessible only by foot or by a 1- to 3-hour boat ride from the nearest road, which was built by a logging company operating in the region. With two exceptions, all participants in the current study were ethnically Bondongo. The final sample for the current study consisted of 16 fathers and all of their available children (total sample size, n = 80 fathers and children). Each man in the sample had at least one child younger than 5-years-old living in their household during the study period. One man's youngest biological child was 10-years-old, but his oldest son lived in the household with his 2-month-old infant. The men all knew each other well, as most had grown up together and/or were related through kinship by various degrees. Two men were relatively recent arrivals: one an immigrant who has lived there for almost 10 years and has a local wife and children; the other arrived more recently along with his wife and children. Both were well integrated into village life.

The Bondongo (singular Mondongo) practice swidden agricultural along the periphery of the tropical forest. In the study village, the primary cultigens include cassava (manioc), plantains, and corn. People also grow taro, peanuts, fruit, and other small crops (Komatsu, 1998). There is a stark sexual division of labor. After men clear the garden plot, agriculture is exclusively women's work. Men organize hunting parties, fish using lines and traps, and cultivate palm wine, or *molenge*. In the study village, there are also two men who are merchants, and one male school teacher. Bondongo culture prescribes a fairly rigid social hierarchy based on gender, age, and status. Compared to women, men wield more overt political power and hold positions of authority in the village government, starting with the Precôt, or elected chief. With a village size of roughly 22 shifting households, most men hold a position on either the council of elders or the council of youth, and the Precôt generally consults with multiple other men, usually the elders, to reach consensus on village decision-making. Regardless of their position in the village hierarchy, all men must also perform subsistence/economic activities to provide for themselves and their families.

2.2. Data collection

Data for this study were collected by AHB and SLL during June and July of 2016. All married men and women with at least one child younger than 18-years-old and their children were eligible for the study. All families available in the village except two agreed to participate. Data from four men and their families were excluded from the current study because of missing data for some relevant measures: Two men left the village on business before salivary data could be collected, one man refused to participate in the saliva component of the study, and one man's children were away from the village during the study period so were not available to provide data on their energetic condition. Village consent to conduct the research was obtained at a public meeting held during a prior field trip in 2015, and individual verbal consent or assent (for children) was obtained from all participants during the 2016 study period. As agreed upon during the public meeting, compensation to each family was in the form of a gift to both the male and female heads of household. Rice, a highly desirable commodity, was also given to each participating family each evening following saliva collection. The study was approved of by the Institutional Review Boards of Duke University (Protocol # 2017-0038) and the University of Notre Dame (# 18-02-4397).

We collected three types of data to assess the relationships between paternal care, children's health and well-being, and testosterone (T):

2.2.1. Paternal Care

As we reported in our initial work from this site (Boyette et al., 2018), we sought to characterize the cultural model of fatherhood among the Bondongo, and to quantify within-group perceptions of individual fathers. We were also interested in local understandings of child health and well-being. First, informal interviews were conducted with adult men and women (n = 14, 36% women) on the subjects of fatherhood and child health and well-being. Responses to the interviews were highly consistent across informants. Using these responses, a set of questions about valued domains of fatherhood and child development was derived to use in a peer-ranking task (von Rueden et al., 2008). The domains of concern here include fathers' indirect care through work as a provider of key resources, direct care of ill children, and direct care in children's socialization, as well as the domain of healthy child growth and development (Table 1).

For the ranking task, men were shown photographs of the other fathers in the study and were then asked to place them in order from first to last in response to each question (Boyette et al., 2018). Participating men were encouraged to uniquely rank their peers, but ties were permitted. For quantitative analysis, the last position in each participant's completed ranking was coded as "1" and the first (highest) as the sum of the number of total positions. Men's rankings of their peers were highly reliable for each question (Cronbach's $\alpha > 0.84$ for each, Table 1). The rankings were then averaged across rankers to establish a score for each man ranked. The two direct care domains were highly correlated ($r = 0.85$, $p < 0.001$) and the average of these two scores was used as a single measure, Direct score, for analysis (Boyette et al., 2018). The inter-correlations between the three ranking variables used in the current study are presented in Table 2a. As can be seen, the two fatherhood quality scores are effectively not correlated, indicating they represent independent domains of fatherhood quality. However, each is significantly, positively correlated with Child Health score. Additionally, Table 2b presents the inter-correlations between the Child Health scores and our measures of children's energetic conditions (see below). Child Health score is significantly and positively correlated with all measures ($p < 0.01$) Together, these inter-correlations suggest that men in the village have shared knowledge of the cultural model of fatherhood, their peer's qualities as direct and indirect caregivers, and the health of each other's families.

Table 2a
Inter-correlation matrix of average peer-ranking scores (Pearson's r values).

	Child Health score	Provider score	Direct score
Child Health score	1.00		
Provider score	0.53^{*}	1.00	
Direct score	0.68^{**}	0.01	1.00

* $p \le 0.05$.
** $p \le 0.01$.

Table 2b
Inter-correlation matrix of average peer-ranking score of children's health and children's age- and sex-adjusted BMI and SFT values (Pearson's r values).

	Child Health score	WFH	BMI	SFT
Child Health score	1.00			
WFH	0.41^{***}	1.00		
BMI	0.35^{**}	0.86^{***}	1.00	
SFT	0.46^{***}	0.38^{**}	0.36^{**}	1.00

** $p < 0.01$.
*** $p < 0.001$.

Risk taking and aspects of Bondongo fathers' care

The greater cultural value placed on indirect paternal care in this community is significant to the current study because those activities in which men engage are risky and could therefore be facilitated by higher T (Goudriaan et al., 2010; Gray et al., 2017; Ronay and von Hippel, 2010; Stanton et al., 2011). For example, fishing involves the risk of drowning in the river or being attacked by crocodiles. Drowning is the most common risk, and we learned of two unexplained drownings along the river by men fishing during the two-month research period. Additionally, clearing the forest for gardens requires felling old growth trees with axes and machetes, burning of the understory, and subsequent routine maintenance by burning. Men's cultivation of *molenge* involves considerable risk but is highly valued and is important in maintaining social relationships and acquiring social status. It is consumed daily and is required at all formal social gatherings. Whose *molenge* is "good" versus "bad" is commonly noted, and men are shamed for serving *molenge* that has been diluted with water. Harvesting *molenge* involves twice daily monitoring of as many as eight palm trees, which are accessible via dugout canoe along the heavily forested banks of the river. The sap is extracted from the top of the tree, which involves climbing by suspending the body with a vine rope or using a vine ladder, typically while carrying a (plastic) wine receptacle, a machete, and other tools (e.g. for making the spout). Falls occur and can lead to severe injury (e.g. concussion, limb breakage). Collectively, these subsistence-related activities do not routinely involve direct male-male competition, but they are important to males' acquisition of status within the relatively hierarchical community and thus could plausibly be linked to T through competition-related pathways as well (Archer, 2006; Gray et al., 2017; Muller, 2017).

2.2.2. *Anthropometrics*

For all available participants, height, weight, and triceps skinfold thickness were measured using standard techniques (Lohman et al., 1988). Height was measured with a Seca stadiometer, and weight with a digital scale. From these measurements, we calculated weight-for-height (WFH) and body mass index (BMI) as indicators of health and energetic status across development. Triceps skinfold thickness (SFT) was measured using Lange skinfold calipers to assess levels of body fat (as a marker of current health and energetic condition). WFH, BMI, and SFT values were adjusted for children's age and sex by regressing each measure on children's age and sex and adding the residuals to the average value of the measure. This method maximized the use of the available data. Due to our relatively small sample size within age groups, common standardization methods such as those used by the WHO (e.g. de Onis et al., 2007) could not be used. However, because it is standard practice to calculate age-adjusted BMI values for children < 2-years-old separately from older children due to differences in the ratio of height to weight during the first two years that can lead to "abnormally" high BMI for the younger group (WHO Multicentre Growth Reference Study Group, 2006), we ran our statistical models both including and excluding children < 2-years-old (n = 3) from the BMI age- and sex-standardization. While the results are qualitatively equivalent, we report only the results that excluded the children < 2 for clarity. For WFH, BMI, and SFT, all adjusted values were transformed to z-scores before statistical analysis.

Table 1
Questions relevant to the current study that were used in the peer-ranking and their associated domain labels.

Domain	Question	Cronbach's α
Child Health score	Whose children are the healthiest?	0.89
Provider (Indirect) score	Who works the hardest?	0.95
Direct score	Sick care sub-domain: Who is most likely to stay home/sacrifice other activities when their children are sick to care for them?	0.85
	Socialization sub-domain: Who "attends to"/"frames" (Fr. encadre) their children's behavior the most?	0.97

2.2.3. Salivary testosterone (T)

All adult men in the study were asked to provide 2 ml of saliva via passive drool, in polypropylene tubes, for up to five evenings. We analyzed 62 total saliva samples for T. Each participant provided a minimum of three samples and all samples were collected within a period of 10 days (see Supplementary methods). Two men (12.5%) gave three samples, 25% gave four, and 62.5% gave five. Along with collection logistic reasons, we focused on evening saliva samples for T because past work in this area has shown that afternoon and evening T tends to be more strongly associated with social dynamics, compared to morning levels (Gettler et al., 2015; Gettler et al., 2012; Gray et al., 2004). Two T data points (one each for two men) were excluded from the analysis based on T values that were 3+ SDs from the mean for the sample as well as 3+ SDs from the mean for the individual participant's T values from the other days. On each day in the presence of the research team, all participants provided saliva roughly between 16:30 and 18:30, thus we minimized between-subject and between-day variability in the time of sampling. Samples were frozen on site in portable liquid nitrogen dewars and kept frozen until they were transported back to the University of Notre Dame (UND) in a liquid nitrogen dry shipper. The samples were then stored at −80 °C at UND until analysis. Samples were analyzed for levels of salivary T using commercially available kits (Salimetrics, Carlsbad, CA; Kit Number: 1-2402) at UND's Hormones, Health, and Human Behavior Lab by MSS under the supervision of LTG. The inter-assay coefficients of variation (CV) for the low and high controls were 9.6% and 5.6%, respectively. The intra-assay CV was 4.6%.

2.3. Statistical analysis

All statistical analyses were conducted using Stata 15.0 (Stata Corporation). The relationships between T and men's fathering qualities and T and children's health were modeled using OLS regression with standard errors clustered by the individual father to account for the repeated sampling of T. This method maximized our use of the available data. All values for T were base-10 log-transformed prior to analysis to adjust for non-normal distribution of the data. To test for the hypothesized inverted U-shaped relationship, the log of men's T levels and the square of this value were entered into a model predicting fathering quality (average rank scores) as the dependent variable—either Provider score, Direct score, or Child Health score. To reduce collinearity and variance inflation in these models, the log of father's T was centered (i.e. the mean was subtracted from each value) before the centered values were then squared (Robinson and Schumacker, 2009). To verify the quadratic nature of the relationship between T and fathering quality/child health, a second set of models were run without log T-squared. Although the pattern appears to vary across populations, older men tend to have lower T than younger males in some settings (Ellison et al., 2002) and this held in our sample. In small-scale societies, men's provisioning effort also tends to be higher in their third and fourth decades of life (Gurven and Hill, 2009), so we included fathers' ages as a covariate in each set of models. For Child Health score, we included a third model that added fathers' Provider and Direct scores, as those are potential pathways through which fathers' T might be predictive of child outcomes. In this model, both Provider and Direct scores were converted to z-scores to allow comparison of the relative effects of each type of paternal care.

OLS regression was also used to test if T had an inverted U-shaped relationship with children's energetic and growth status, and if this relationship was accounted for by fatherhood quality. Standard errors were clustered by household to control for non-independence of measurements. For this analysis, three sets of models were tested in sequence with each child health indicator (WFH, BMI, and SFT) as the outcome variable. The average level of T was calculated for each father, log base 10 transformed, and then included as a predictor in each set of models. The log of fathers' T was again centered before the square values were calculated. In the first model, the log of fathers' T, its squared value, and fathers' ages were included as predictors. In the second model, the log of T-squared was removed to compare the quadratic with the linear relationship between fathers' T and child health. Finally, fathers' Provider and Direct scores were included in a third model to test whether paternal care was potentially in the pathway between T and child outcomes. Again, both Provider and Direct scores were converted to z-scores to enable comparison of relative effect sizes.

For both sets of models, children's age, children's sex, fathers' total number of biological children, number of children in the household, age of fathers' youngest child, and fathers' energetic status (fathers' triceps SFT) were examined as potential covariates. Given the relatively small sample size for our study, which increases potential risk related to overfitting of models, covariates with a non-significant association to our predictor variable (fathers' T) were excluded from the final models but the relevant bivariate relationships are presented in Table S2.

3. Results

The mean age of fathers in our study ($n = 16$) was 37.19 years old ($SD = 8.15$), and they had an average of 6 children ($SD = 3.68$). Assessed from 60 total samples, the mean T for the fathers was 76.02 pg/ml ($SD = 36.48$). Older men had lower T ($r = -0.40$, $p = 0.002$), with a similar negative correlation between age and log T ($r = -0.33$, $p = 0.01$). As fathering quality was measured by a peer-ranking task, it is notable that the range for our measure of indirect care (i.e. Provider Score) was about twice as large as that for our measure of direct care (i.e. Direct Score), indicating men made more fine-grained distinctions between their peers when assessing the quality of their indirect care. Further descriptive statistics are presented in Table 3.

In our first set of models, which tested for an inverted U-shaped relationship between fathers' T and their indirect care rankings (i.e. Provider score), the regression results were consistent with a linear relationship, as men with higher log T had significantly greater Provider scores in Model 1 ($p = 0.010$) and Model 2 ($p = 0.017$; Table 4; Fig. 1) but log T-squared ($p = 0.486$) and was not statistically significant in Model 1 (Table 4). Fig. 1 displays the linear relationship.

In our second set of models, we performed the same analysis as above but tested whether there was an inverted U-shaped versus a linear relationship between fathers' T and their quality as direct care providers (i.e. Direct score). While we predicted there would not be a significant association between T and men's direct care, we found limited evidence for an inverted U-shaped relationship, as the quadratic term in the model was statistically significant whereas the linear term

Table 3
Descriptive statistics.

	n	Mean	SD	Min	Max
Fathers					
T (pg/ml)[a]	16	76.02	36.48	27.06	171.43
Age (years)	16	37.19	8.15	24.00	50.00
Age of spouse(s) (years)[b]	16	33.00	8.05	18.00	48.00
Number of children	16	6.06	3.68	1.00	15.00
Provider Score	16	8.44	3.67	1.60	15.38
Direct Score	16	4.83	2.01	1.39	8.42
Child Health Score	16	5.90	2.26	2.19	9.50
Children					
Age (years)	64	8.02	4.27	1.00	17.00
WFH (kg/cm)	64	0.19	0.02	0.15	0.26
BMI (kg/m^2)[c]	61	15.94	1.52	13.21	19.74
SFT (mm)[c]	58	9.36	3.17	4.00	19.00
Biological child (% yes)	64	87.50	–	0	1

[a] Values for T are derived from 60 total data points from the 16 participants.
[b] Values include co-wives of one man; one participating man's wife refused to participate.
[c] Values adjusted for children's age and sex.

Table 4
Tests of relationships between quality of indirect care (i.e. Provider Score) and fathers' T.

	Model 1: $R^2 = 0.29$			Model 2: $R^2 = 0.28$		
	b	SE	p	b	SE	p
Log T[a]	6.19	2.12	0.010	5.95	2.23	0.017
Log T-squared	-5.36	7.50	0.486			
Age	0.24	0.12	0.062	0.25	0.12	0.049

[a] Log T and log T-squared reflect centered values.

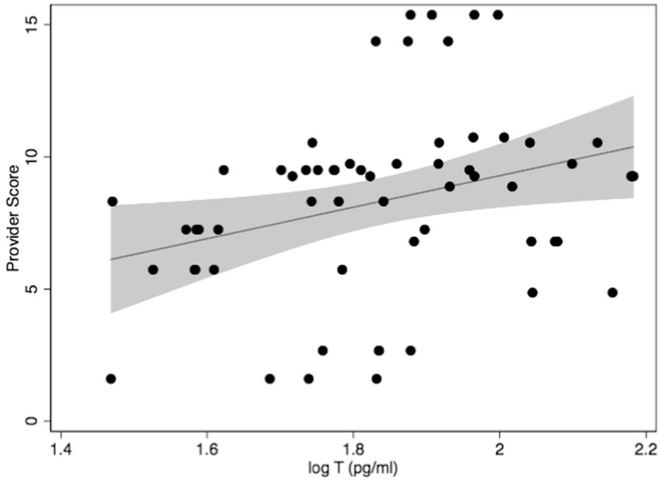


Fig. 1. Linear fit plot with 95% confidence intervals of the log of fathers' salivary T predicting the average ranking of their quality as providers. Scatter plot of log T data adjusted for father's age is overlaid.

was not (log T: $p = 0.926$; log T-squared: $p = 0.033$; Table 5; Fig. 2) controlling for fathers' ages. As can be seen in Fig. 2, the curvature of the best fit line between log T and fathers' Direct Score is modest. While this significant quadratic relationship obviates the need to test for a linear correlation, we note that Model 2 (Table 5) showed no significant linear relationship for these variables ($p = 0.919$).

In the next set of models, we tested for links between fathers' T and children's health as measured by the ranking task and anthropometrics, respectively, and whether father's indirect and direct caregiving helped to account for those relationships. Similar to the results above for fathers' direct care, we found limited evidence for a quadratic relationship between fathers' log T and the rankings of their children's health (log T: $p = 0.394$; log T-squared: $p = 0.029$, Model 1, Table 6), controlling for fathers' ages (Fig. 3). Moreover, we found that fathers' Direct and Provider scores attenuated this relationship (Model 3, Table 6). In Model 3, both ranking scores were statistically significant, with a relatively larger effect size (b) for direct care (Direct: $p < 0.001$; Provider: $p = 0.001$; Table 6), the quadratic term for fathers' log T was no longer significant, and the (absolute) magnitude of the effect size (b) diminished substantially ($p > 0.4$).

In modeling children's anthropometrics, we found an inverted U-shaped relationship between fathers' log T and their children's BMI z-scores (log T: $p = 0.003$; log T-squared: $p = 0.013$) and triceps skinfold thickness (SFT) z-scores (log T: $p = 0.009$; log T-squared: $p = 0.030$), independent of fathers' ages (Table 7, Fig. 4). Given the significant findings for the quadratic models, it was not necessary to proceed with the alternative linear modeling approach, but we present those non-significant results for comparison in Table 7 for BMI and SFT (Model 2: both $p > 0.05$). As with the analysis of fathers' rankings of children's health, there was also evidence that paternal care was potentially in the pathway for these findings (Model 3, Table 7). For BMI, the addition of the two paternal care rankings strongly reduced the (absolute) magnitude of the effect size (b) for log T-squared, which was no longer statistically significant ($p > 0.5$), although we note that both ranking scores were also non-significant (both $p > 0.3$). The linear term remained statistically significant with a similar effect size (b) ($p = 0.012$). In Model 3 for children's SFT, both direct care (i.e. Direct score) and indirect care (i.e. Provider score) were statistically significant, with a larger relative effect size for direct care (both $p < 0.05$; Table 7). In this model, the linear and quadratic terms for fathers' log T were no longer significant and had reduced effect sizes (b) compared to Model 1 (both $p > 0.1$; Table 7). Children's weight-for-height (WFH) z-scores were also examined, but there was no significant quadratic or linear relationship found between fathers' T and children's WFH (all $p > 0.1$).

4. Discussion

In this paper, we aimed to shed light on the relationships between men's T, their fathering quality, and their children's health (i.e. via local perceptions and measures of energetic status). Our results show that fathers with higher T than other fathers in their community tended to be ranked as better providers. However, we also found that fathers with medium range T (for their community) were generally viewed as being better direct caregivers and were ranked as having healthier children, though those relationships were modest. In a similar, but relatively more robust set of findings, fathers with medium-range T had children who were in better energetic condition based on anthropometric measures; those associations were largely accounted for by fathers' direct and indirect caregiving. Our findings help shed light on the function of one of the key physiological mechanisms (T) thought to play a role in mediating male life history trade-offs, and our results specifically contribute new insights on how men's T relates to parenting effort in ecologies in which there are overlaps between risky behavior and fathers' contributions to families. In particular, our findings provide insights on fitness-relevant behaviors (i.e. provisioning) and outcomes (i.e. improved child health and energetics) linked to fathers' T in such an ecological context, which is evolutionarily-relevant to the emergence of human's unique life history strategy.

In the current study, we first tested for relationships between fathers' T and their levels of indirect care of their children, as measured by peer-rankings of their quality as hard-working providers of key resources. The fathers who were ranked as the best providers in this community were those who had higher T compared to their fellow fathers, which, to our knowledge, is the first time that a measure of fathers' indirect care has been linked to basal T, including in small-scale, subsistence-level societies. Bondongo men's valued work, including fishing, hunting, felling trees and burning new garden plots, and collecting palm wine, are all risky activities. These activities are also associated with men's status and comparable activities are linked to higher fitness in small-scale societies (von Rueden and Jaeggi, 2016). Thus, these results align with conceptual frameworks and past findings regarding T's role in motivating risky and competitive behaviors, which are often mating-related, including among humans and other vertebrates (Gray et al., 2017; Muller, 2017; van Anders, 2013). They could

Table 5
Tests of relationships between quality of direct care (i.e. Direct Score) and fathers' T.

	Model 1: $R^2 = 0.12$			Model 2: $R^2 = 0.08$		
	b	SE	p	b	SE	p
Log T[a]	0.19	2.05	0.926	-0.22	2.12	0.919
Log T-squared	-9.34	3.98	0.033			
Age	0.05	0.06	0.425	0.07	0.05	0.231

[a] Log T and log T-squared reflect centered values.

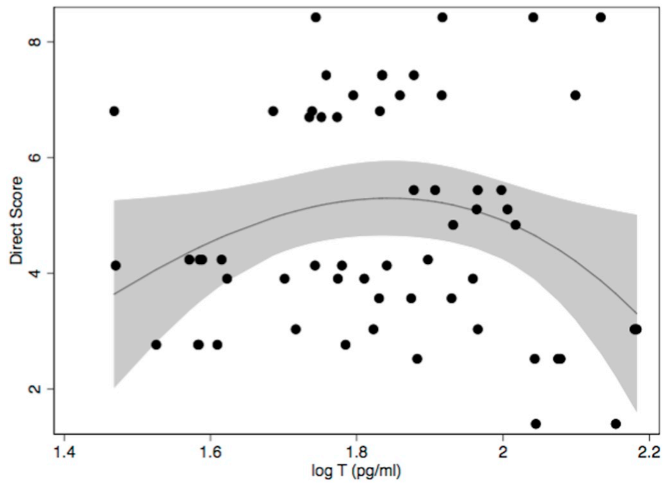


Fig. 2. Fractional polynomial fit plot with 95% confidence intervals of the log of fathers' salivary T predicting the average ranking of their quality as direct caregivers. Scatter plot of log T data adjusted for father's age is overlaid.

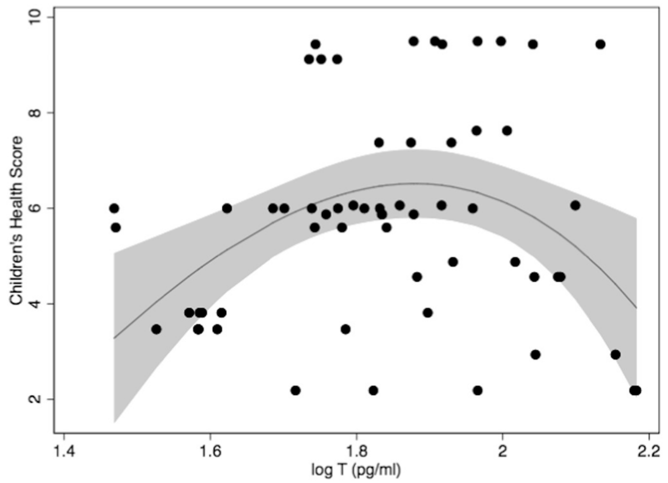


Fig. 3. Fractional polynomial fit plot with 95% confidence intervals of the log of fathers' salivary T predicting the average ranking of their children's health. Scatter plot of log T data adjusted for father's age is overlaid.

plausibly relate to T indirectly through competition- and status-seeking pathways, despite not typically involving overt male-male competition. Indeed, in hierarchical social contexts, highly ranked, dominant male primates, including humans, often have elevated T (Muller, 2017).

Our results also show some broad complementarity to past work in Tanzania and Kenya, respectively, on men's T and life history status in subsistence-level societies in which fathers are minimally involved with direct care of young children, fathers contribute primarily via indirect care, and polygyny is culturally sanctioned. Muller et al. (2009) found that among Datoga pastoralists fathers and non-fathers did not differ significantly for T, while Gray (2003) showed that Kenyan Swahili men with multiple wives had higher T than other men. While there are important design differences between those studies and ours, they are consistent with the notion that when aspects of men's partnering/parenting effort overlap with mating effort and/or involve competition and risk taking, men succeeding in those roles will likely have elevated T. In a pair of studies among Tsimane forager-horticulturalists in Bolivia, it was shown that men's T acutely spiked during intensive subsistence labor (tree chopping for plot clearing) as well as around the time they made a kill while hunting. Trumble and colleagues interpreted those patterns as potentially facilitating enhanced muscular metabolic processes (tree chopping) or reward-based effects of T (hunting) related to provisioning (Trumble et al., 2014; Trumble et al., 2013). Given the different time scale of those studies (short-term hormone changes) relative to ours (basal hormone levels), there are no specific contradictions between their interpretations and our findings or framing, and we would argue they are potentially complementary. Meanwhile, research elsewhere among rural Polish men in a community practicing subsistence, non-mechanized agriculture found that partnered fathers had lower T than other men but also worked more than them (Alvarado et al., 2015). That team found negative bivariate relationships between men's T and workload, although they were modest and not significant. While further comparison between our results and those of Alvarado et al.' (2015) are constrained by divergences in design, these relative differences at least suggest that there could be variation by type/nature of subsistence labor, ecology, and culture that shape relationships between fathers' indirect care and T (see also Gettler et al., 2015).

From an a priori perspective, it was plausible that fathers with middle-range T could have been ranked more highly as providers in this context (an inverted U-shaped relationship), which was our alternative hypothesis. This possibility aligns with some evidence from animal models but has not been shown in humans. For example, experimental results from animal models suggest that when males' T is elevated too much during periods in which they would otherwise cooperate with mothers to care for young, they forego parental care and focus their reproductive effort on pursuing females and competing with other males for extra-pair opportunities (Ketterson et al., 1992; Reed et al., 2006). While our results here suggest that fathers' elevated T may not conflict with indirect forms of parenting effort, it is also possible that Bondongo men's provisioning activities may also serve to advertise men's qualities as mates.

Diverging from the patterns for indirect care, our findings support a modest inverted U-shaped relationship between fathers' T and their rankings as direct caregivers. Many of the prior studies linking lower paternal T to greater engagement in direct care come from societies in which fathers' nurturant, hands-on caregiving is more prevalent and valued than among the Bondongo (Edelstein et al., 2017; Gettler et al., 2011; Mascaro et al., 2013; Weisman et al., 2014). Thus, given the cultural setting for our study and based on existing frameworks (Gettler, 2016a; van Anders et al., 2011; van Anders, 2013), we

Table 6
Tests of relationships between children's health rankings (Child Health Score) and fathers' T.

	Model 1: $R^2 = 0.31$			Model 2: $R^2 = 0.27$			Model 3: $R^2 = 0.74$		
	b	SE	p	b	SE	p	b	SE	p
Log T[a]	1.76	2.01	0.394	1.28	2.19	0.566	-0.17	1.32	0.896
Log T-squared	-10.77	4.45	0.029				-2.27	2.65	0.404
Age	0.14	0.05	0.010	0.16	0.04	0.003	0.03	0.04	0.455
Provider z-score							1.07	0.27	0.001
Direct z-score							1.48	0.31	0.0002

[a] Log T and log T-squared reflect centered values.

Table 7
Tests of relationships between fathers' T and children's BMI (top) and SFT (bottom).

BMI z-score (n = 61)	Model 1: $R^2 = 0.19$			Model 2: $R^2 = 0.12$			Model 3: $R^2 = 0.19$		
	b	SE	p	b	SE	p	b	SE	p
Log T[a]	2.74	0.76	0.003	2.29	1.14	0.065	2.49	0.86	0.012
Log T-squared	−15.29	5.34	0.013				−6.93	10.52	0.521
Fathers' age	0.02	0.02	0.294	0.05	0.02	0.008	0.03	0.03	0.342
Provider z-score							0.07	0.18	0.715
Direct z-score							0.20	0.18	0.284

SFT z-score (n = 58)	Model 1: $R^2 = 0.22$			Model 2: $R^2 = 0.09$			Model 3: $R^2 = 0.35$		
	b	SE	p	b	SE	p	b	SE	p
Log T[a]	2.79	0.92	0.009	2.14	1.25	0.108	1.54	0.94	0.125
Log T-squared	−21.99	9.11	0.030				3.31	7.39	0.661
Fathers' age	0.00	0.03	0.912	0.05	0.02	0.072	0.01	0.02	0.496
Provider z-score							0.33	0.12	0.017
Direct z-score							0.54	0.10	0.0001

[a] Log T and log T-squared reflect centered values.

predicted that we would not find a significant relationship between fathers' T and direct care. In contrast, our results hint that fathers with medium-range T for this community were rated as better direct caregivers. While unanticipated, these results do align conceptually with recent findings showing that when father's T is too low they may be prone to depression (which could interfere with direct or indirect parenting effort) and/or reduced direct care (Gettler et al., 2017; Saxbe et al., 2017). While average levels of direct caregiving across fathers at this site are low, including by cross-cultural standards (Hewlett and Macfarlan, 2010; Gray and Anderson, 2010), there is between-father variation for engagement in these behaviors, particularly as children move beyond weaning age and into later stages of childhood. Unfortunately, we do not have direct behavioral observations of men's parenting in this study, which is a limitation (see below), to verify the range of variation in duration/frequency/type of men's direct care. Because the quadratic term was statistically significant in the model for this finding, whereas the linear term was not, we are hesitant to overemphasize the importance of this result, but suggest this hypothesis merits further testing at other sites, given the complementarity with other recent results (Gettler et al., 2017).

Similarly, we found evidence for an inverted U-shaped relationship between fathers' T and children's well-being, particularly as indicated by anthropometric measures of children's energetic status. Our results here specifically demonstrate that fathers with middle-range T had children with better energetic status, as measured by both BMI and triceps SFT. As we outlined in the Introduction, among vertebrates with biparental care, it is relatively common for males to have lower T when they cooperate with females to care for offspring, particularly in species in which paternal care is facultative and not obligate (Lynn, 2008). This leads to the prediction that lower paternal T would tend to be linked to increased offspring survival and quality. Consistent with this idea, research in birds with biparental care shows fathers with experimentally elevated T experience higher rates of offspring mortality (Reed et al., 2006). These potential associations have been little tested in other vertebrate taxa.

As we have noted above, this is further complicated in humans because fathers with too low of T are prone towards poorer mental health and reduced parenting effort (Gettler et al., 2017; Saxbe et al., 2017), but those with more modestly reduced T tend to engage in greater direct care (Gettler, 2014, 2016a; Gray et al., 2017; van Anders, 2013). Meanwhile, human males with elevated T or androgen function also tend to experience relationship disruption (Gettler et al., 2017;

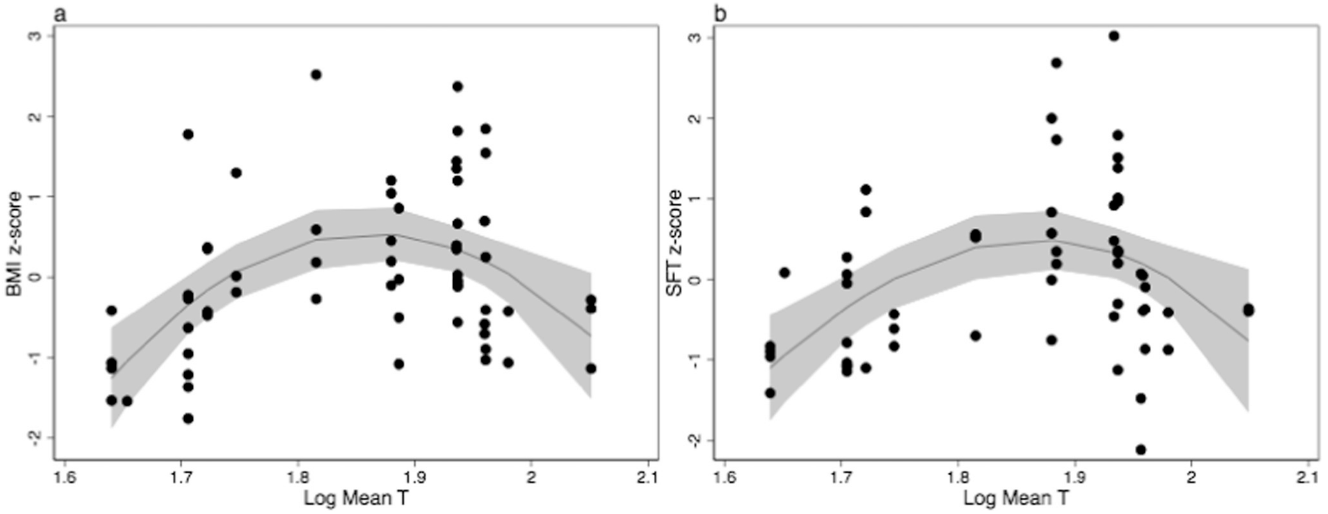


Fig. 4. Fractional polynomial fit plots with 95% confidence intervals of the average of the log of fathers' salivary T predicting children's a) BMI and b) triceps SFT z-scores. Scatter plot of log T data adjusted for father's age is overlaid.

Mazur and Michalek, 1998) and lower relationship satisfaction and commitment for themselves and their partners (Edelstein et al., 2014), all of which could also negatively impact children's well-being, especially in harsh and challenging ecologies. These prior results are consistent with the notion that whether forms of paternal care that are ecologically critical and culturally salient skew more towards direct or indirect care (and combinations thereof), fathers with T that is in a moderate range, avoiding low and high extremes, may have children with the most optimal outcomes. Our findings suggest that these patterns linking fathers' T to child energetic condition were largely explained by fathers' rankings for direct and indirect care, which align with conceptual models of fathers' contributions to child outcomes and their underlying psychobiological pathways as well as past results from this site and others for child health (Boyette et al., 2018; Gettler, 2014; Gray and Anderson, 2010; Gurven and Hill, 2009; Kaplan et al., 2000; Rosenbaum and Gettler, 2018; Winking and Koster, 2015). To our knowledge, our results are the first to link human fathers' T to their children's health, and specifically to energetic status, which is critical to their long-term growth, development, and survival (Martorell et al., 2010; Nandy et al., 2005). Through those pathways, our findings help provide some of the first evidence linking profiles of fathers' T to fitness-relevant outcomes in their children.

Complementing the patterns we found here, we note that in our prior publication on these data (Boyette et al., 2018) we also observed stronger links between fathers' direct care rankings and child energetics, compared to associations with fathers' indirect care rankings. The pathways linking fathers' direct caregiving to child energetics are conceptually less clear than would be the case for indirect care, especially provisioning. Consequently, it is plausible that fathers' Direct scores are correlated with or index other unmeasured factors related to family life beyond fathers' own care that are likely to influence child health and development in this community. For example, research in other small-scale settings has found that marital partners' work effort is positively correlated (Gurven et al., 2009) and assortative mating is common, such that men and women of similar quality tend to partner (Smith, 2004). It is plausible that men with moderate levels of T are preferred by females as partners because they may tend towards social functioning that is more optimal for long-term cooperation and family life (i.e. less inclined towards anger; more empathetic) compared to higher T men (Gettler, 2016b), but they are also relatively better providers and higher in status than lower T males. In the current case, it may be that women's contributions to indirect and direct care, while somewhat matched to those of their partners, matter more for child health. Alternatively, or in addition, men with medium range T could improve their children's health through building and maintaining social network ties (e.g. gathering and sharing palm wine or meat, participating in work parties, or recruiting/cultivating alloparental care) in ways that support their children's energetic status via pathways other than fathers directly caring for or provisioning them (Gettler, 2016b; von Rueden et al., 2008). For example, in other settings, reputations for both competency and cooperation tend to yield benefits for men and their families in terms of health (Macfarlan and Lyle, 2015).

Our study has a number of limitations that merit discussion. First, our sample size is small, especially for fathers, which limits statistical power and can also pose issues for statistical models with polynomial terms. This is simply a reality of working at this very remote, difficult to access field site with participants residing in a small community. Our sample of 16 fathers represents ~89% of the potential fathers who were present at the site for the duration of the data collection period. We attempted to mitigate some of these inherent limitations by conducting repeated sampling for fathers' T, using data analytical approaches that maximized the use of those repeated measurements, and recruiting a comparatively larger sample of men's children. Second, all of our data are cross-sectional and our analyses could have been further clarified by additional variables regarding family life. Both of these dynamics contribute to a greater possibility of confounding than if our design were longitudinal and/or a bit more expansive. For example, as we mentioned above, we were not able to rule out maternal care or care from others as factors that might help explain links between fathers' T and child energetic condition. In addition, while we found interrelationships between fathers' T, paternal caregiving, and their children's BMI and SFT, we did not find similar associations between fathers' T and children's WFH. We can only speculate on why this might be the case. In our sample, children's WFH was more strongly positively correlated with their height than was BMI or SFT. Early life nutritional and morbidity exposures particularly help shape trajectories for height (Adair, 2007; Wells et al., 2005), so perhaps the longer-term factors shaping children's WFH are more decoupled from pathways related to fathers' T, which likely facultatively varies through time. Furthermore, we were not able to independently measure men's indirect or direct care by way of systematic behavioral observation. While the high reliability of our peer-rankings (see Methods) gives us confidence they were accurate representations of relative quality of care, observational measures of time spent in resource acquisition (along with quantitative assessment of economic returns), direct caregiving, and social network maintenance would help clarify the connection between men's T, fathering quality, and child outcomes. Measurement of mothers' and others' direct and indirect care and contributions to child health and the connections between men's T profiles and measures of their social networks across multiple domains would be fruitful areas of future research, and we hope to help clarify these remaining questions in subsequent field seasons.

5. Conclusions

Overall, this study advances our knowledge of the complex ways in which T interrelates with aspects of men's life history strategies, particularly forms of indirect parenting effort, which may overlap with risk taking and competitive behaviors as well as status acquisition in some small-scale societies. To our knowledge, our results are the first to link elevated T among fathers to greater provisioning and indirect care (or perceptions thereof). However, notably, they also provide the new insight that fathers with more medium-range T have children in better energetic condition, which is largely accounted for by their parenting effort. These novel results add further support to the view that men's life history strategies are flexible, and that T acts to facilitate male reproductive strategies in context-dependent ways across human socioecologies (Gettler, 2014, 2016a; van Anders, 2013).

Acknowledgments

We offer our immense gratitude to those in Congo who helped facilitate this research: The Institut National de Recherche en Sciences Exactes et Naturelles (IRSEN), especially Dr. Clobite Bouka-Biona; the Centre de Recherche et D'Edudes en Sciences Sociales et Humaines (CRESSH), especially Dr. Francois Ibara; Dzabatou Moise and Mindula Koutain for their assistance with fieldwork; and Precôt Claude-Alain, Secrétaire Alain-Nicaise, and the Bondongo families who made the study possible.

Funding

This work was supported by the Jacobs Foundation. LTG was funded by a Wenner-Gren Foundation Hunt Postdoctoral Writing Fellowship and MSS by a National Science Foundation Graduate Research Fellowship during portions of the research for this project.

Declaration of competing interest

The authors declare no competing interests.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.yhbeh.2018.09.006.

References

Adair, L.S., 2007. Size at birth and growth trajectories to young adulthood. Am. J. Hum. Biol. 19, 327–337. https://doi.org/10.1002/ajhb.20587.

Alvarado, L.C., Muller, M.N., Emery Thompson, M., Klimek, M., Nenko, I., Jasienska, G., 2015. The paternal provisioning hypothesis: effects of workload and testosterone production on men's musculature: male provisioning, testosterone, and musculature. Am. J. Phys. Anthropol. 158, 19–35. https://doi.org/10.1002/ajpa.22771.

van Anders, S.M., 2013. Beyond masculinity: testosterone, gender/sex, and human social behavior in a comparative context. Front. Neuroendocrinol. 34, 198–210. https://doi.org/10.1016/j.yfrne.2013.07.001.

van Anders, S.M., Goldey, K.L., 2010. Testosterone and partnering are linked via relationship status for women and 'relationship orientation' for men. Horm. Behav. 58, 820–826. https://doi.org/10.1016/j.yhbeh.2010.08.005.

van Anders, S.M., Goldey, K.L., Kuo, P.X., 2011. The steroid/peptide theory of social bonds: integrating testosterone and peptide responses for classifying social behavioral contexts. Psychoneuroendocrinology 36, 1265–1275. https://doi.org/10.1016/j.psyneuen.2011.06.001.

Archer, J., 2006. Testosterone and human aggression: an evaluation of the challenge hypothesis. Neurosci. Biobehav. Rev. 30, 319–345. https://doi.org/10.1016/j.neubiorev.2004.12.007.

Bales, K.L., Saltzman, W., 2016. Fathering in rodents: neurobiological substrates and consequences for offspring. Horm. Behav. 77, 249–259. https://doi.org/10.1016/j.yhbeh.2015.05.021.

Boyette, A.H., Lew-Levy, S., Gettler, L.T., 2018. Dimensions of fatherhood in a Congo Basin village: a multi-method analysis of intra-cultural variation in men's parenting and its relevance for child health. Curr. Anthropol. 59 (6).

Bribiescas, R.G., 2001. Reproductive ecology and life history of the human male. Am. J. Phys. Anthropol. 116, 148–176. https://doi.org/10.1002/ajpa.10025.

Clutton-Brock, T.H., 1991. The Evolution of Parental Care, Monographs in Behavior and Ecology. Princeton University Press, Princeton, N.J.

Desjardins, J.K., Stiver, K.A., Fitzpatrick, J.L., Milligan, N., Van Der Kraak, G.J., Balshine, S., 2008. Sex and status in a cooperative breeding fish: behavior and androgens. Behav. Ecol. Sociobiol. 62, 785–794. https://doi.org/10.1007/s00265-007-0504-1.

Edelstein, R.S., Chopik, W.J., Kean, E.L., 2011. Sociosexuality moderates the association between testosterone and relationship status in men and women. Horm. Behav. 60, 248–255. https://doi.org/10.1016/j.yhbeh.2011.05.007.

Edelstein, R.S., van Anders, S.M., Chopik, W.J., Goldey, K.L., Wardecker, B.M., 2014. Dyadic associations between testosterone and relationship quality in couples. Horm. Behav. 65, 401–407. https://doi.org/10.1016/j.yhbeh.2014.03.003.

Edelstein, R.S., Chopik, W.J., Saxbe, D.E., Wardecker, B.M., Moors, A.C., Labelle, O.P., 2017. Prospective and dyadic associations between expectant parents' prenatal hormone changes and postpartum parenting outcomes. Dev. Psychobiol. 59, 77–90. https://doi.org/10.1002/dev.21469.

Ellison, P.T., Bribiescas, R.G., Bentley, G.R., Campbell, B.C., Lipson, S.F., Panter-Brick, C., Hill, K., 2002. Population variation in age-related decline in male salivary testosterone. Hum. Reprod. 17, 3251–3253. https://doi.org/10.1093/humrep/17.12.3251.

Gettler, L.T., 2010. Direct male care and hominin evolution: why male-child interaction is more than a nice social idea. Am. Anthropol. 112, 7–21. https://doi.org/10.1111/j.1548-1433.2009.01193.x.

Gettler, L.T., 2014. Applying socioendocrinology to evolutionary models: fatherhood and physiology. Evol. Anthropol. Issues News Rev. 23, 146–160. https://doi.org/10.1002/evan.21412.

Gettler, L.T., 2016a. Becoming DADS: considering the role of cultural context and developmental plasticity for paternal socioendocrinology. Curr. Anthropol. 57, S38–S51. https://doi.org/10.1086/686149.

Gettler, L.T., 2016b. Testosterone, fatherhood and social networks. In: Trevathan, W.R., Rosenberg, K.L. (Eds.), Costly and Cute: How Helpless Newborns Made Us Human. School for Advanced Research, Santa Fe, N.M, pp. 146–176.

Gettler, L.T., McDade, T.W., Feranil, A.B., Kuzawa, C.W., 2011. Longitudinal evidence that fatherhood decreases testosterone in human males. Proc. Natl. Acad. Sci. 108, 16194–16199. https://doi.org/10.1073/pnas.1105403108.

Gettler, L.T., McKenna, J.J., McDade, T.W., Agustin, S.S., Kuzawa, C.W., 2012. Does cosleeping contribute to lower testosterone levels in fathers? Evidence from the Philippines. PLoS One 7.

Gettler, L.T., McDade, T.W., Agustin, S.S., Feranil, A.B., Kuzawa, C.W., 2015. Longitudinal perspectives on fathers' residence status, time allocation, and testosterone in the Philippines. Adapt. Human Behav. Physiol. 1, 124–149. https://doi.org/10.1007/s40750-014-0018-9.

Gettler, L.T., Ryan, C.P., Eisenberg, D.T.A., Rzhetskaya, M., Hayes, M.G., Feranil, A.B., Bechayda, S.A., Kuzawa, C.W., 2017. The role of testosterone in coordinating male life history strategies: the moderating effects of the androgen receptor CAG repeat polymorphism. Horm. Behav. 87, 164–175. https://doi.org/10.1016/j.yhbeh.2016.10.012.

Goudriaan, A.E., Lapauw, B., Ruige, J., Feyen, E., Kaufman, J.-M., Brand, M., Vingerhoets, G., 2010. The influence of high-normal testosterone levels on risk-taking in healthy males in a 1-week letrozole administration study. Psychoneuroendocrinology 35, 1416–1421. https://doi.org/10.1016/j.psyneuen.2010.04.005.

Goymann, W., Landys, M.M., Wingfield, J.C., 2007. Distinguishing seasonal androgen responses from male–male androgen responsiveness—revisiting the challenge hypothesis. Horm. Behav. 51, 463–476.

Gray, P.B., 2003. Marriage, parenting, and testosterone variation among Kenyan Swahili men. Am. J. Phys. Anthropol. 122, 279–286. https://doi.org/10.1002/ajpa.10293.

Gray, P.B., Anderson, K.G., 2010. Fatherhood: Evolution and Human Paternal Behavior. Harvard University Press, Cambridge, Mass.

Gray, P.B., Campbell, B.C., Marlowe, F.W., Lipson, S.F., Ellison, P.T., 2004. Social variables predict between-subject but not day-to-day variation in the testosterone of US men. Psychoneuroendocrinology 29, 1153–1162. https://doi.org/10.1016/j.psyneuen.2004.01.008.

Gray, P.B., McHale, T.S., Carré, J.M., 2017. A review of human male field studies of hormones and behavioral reproductive effort. Horm. Behav. 91, 52–67. https://doi.org/10.1016/j.yhbeh.2016.07.004.

Gurven, M., Hill, K., 2009. Why do men hunt?: a reevaluation of "man the hunter" and the sexual division of labor. Curr. Anthropol. 50, 51–74. https://doi.org/10.1086/595620.

Gurven, M., Winking, J., Kaplan, H., von Rueden, C., McAllister, L., 2009. A bioeconomic approach to marriage and the sexual division of labor. Hum. Nat. 20, 151–183. https://doi.org/10.1007/s12110-009-9062-8.

Hau, M., 2007. Regulation of male traits by testosterone: implications for the evolution of vertebrate life histories. BioEssays 29, 133–144. https://doi.org/10.1002/bies.20524.

Hawkes, K., Bliege Bird, R., 2002. Showing off, handicap signaling, and the evolution of men's work. Evol. Anthropol. Issues News Rev. 11, 58–67. https://doi.org/10.1002/evan.20005.

Hawkes, K., O'Connell, J.F., Blurton Jones, N.G., 2001. Hunting and nuclear families: some lessons from the Hadza about mens work. Curr. Anthropol. 42, 681–709. https://doi.org/10.1086/322559.

Hewlett, B.S., Macfarlan, S.J., 2010. Fathers' roles in hunter-gatherer and other small-scale cultures. In: Lamb, M.E. (Ed.), The Role of the Father in Child Development. John Wiley and Sons, Inc., New Jersey, pp. 413–434.

Hirschenhauser, K., Oliveira, R.F., 2006. Social modulation of androgens in male vertebrates: meta-analyses of the challenge hypothesis. Anim. Behav. 71, 265–277. https://doi.org/10.1016/j.anbehav.2005.04.014.

Kaplan, H.S., Hill, K., Lancaster, J., Hurtado, M., 2000. A theory of human life history evolution: diet, intelligence, and longevity. Evol. Anthropol. Issues News Rev. 9, 156–185.

Ketterson, E.D., Nolan, V., Wolf, L., Ziegenfus, C., 1992. Testosterone and avian life histories: effects of experimentally elevated testosterone on behavior and correlates of fitness in the dark-eyed junco (*Junco hyemalis*). Am. Nat. 140, 980–999.

Komatsu, K., 1998. The food cultures of the shifting cultivators in Central Africa: the diversity in selection of food materials. In: African Study Monographs, Supplement 25, pp. 149–177.

Lawson, D.W., Schaffnit, S.B., Hassan, A., Ngadaya, E., Ngowi, B., Mfinanga, S.G.M., James, S., Borgerhoff Mulder, M., 2017. Father absence but not fosterage predicts food insecurity, relative poverty, and poor child health in northern Tanzania. Am. J. Hum. Biol. 29, e22938. https://doi.org/10.1002/ajhb.22938.

Lohman, T.G., Roche, A.F., Martorell, R., 1988. Anthropometric Standardization Reference Manual. Human Kinetics Publishers, Inc., Champaign, IL.

Lukas, D., Clutton-Brock, T., 2013. The evolution of social monogamy in mammals. Science 341, 526–530.

Lynn, S.E., 2008. Behavioral insensitivity to testosterone: why and how does testosterone alter paternal and aggressive behavior in some avian species but not others? Gen. Comp. Endocrinol. 157, 233–240.

Macfarlan, S.J., Lyle, H.F., 2015. Multiple reputation domains and cooperative behaviour in two Latin American communities. Philos. Trans. R. Soc., B 370, 20150009. https://doi.org/10.1098/rstb.2015.0009.

Marlowe, F.W., 1999. Showoffs or providers? The parenting effort of Hadza men. Evol. Hum. Behav. 20, 391–404.

Martorell, R., Melgar, P., Maluccio, J.A., Stein, A.D., Rivera, J.A., 2010. The nutrition intervention improved adult human capital and economic productivity. J. Nutr. 140, 411–414. https://doi.org/10.3945/jn.109.114504.

Mascaro, J.S., Hackett, P.D., Rilling, J.K., 2013. Testicular volume is inversely correlated with nurturing-related brain activity in human fathers. Proc. Natl. Acad. Sci. U. S. A. 110, 15746–15751.

Mazur, A., Michalek, J., 1998. Marriage, divorce, and male testosterone. Soc. Forces 77, 315–330.

McDade, T.W., Reyes-García, V., Tanner, S., Huanca, T., Leonard, W.R., 2008. Maintenance versus growth: investigating the costs of immune activation among children in lowland Bolivia. Am. J. Phys. Anthropol. 136, 478–484. https://doi.org/10.1002/ajpa.20831.

McIntyre, M., Gangestad, S.W., Gray, P.B., Chapman, J.F., Burnham, T.C., O'Rourke, M.T., Thornhill, R., 2006. Romantic involvement often reduces men's testosterone levels—but not always: the moderating role of extrapair sexual interest. J. Pers. Soc. Psychol. 91, 642–651. https://doi.org/10.1037/0022-3514.91.4.642.

Muehlenbein, M.P., Bribiescas, R.G., 2005. Testosterone-mediated immune functions and male life histories. Am. J. Hum. Biol. 17, 527–558. https://doi.org/10.1002/ajhb.20419.

Muller, M.N., 2017. Testosterone and reproductive effort in male primates. Horm. Behav. 91, 36–51. https://doi.org/10.1016/j.yhbeh.2016.09.001.

Muller, M.N., Marlowe, F.W., Bugumba, R., Ellison, P.T., 2009. Testosterone and paternal care in East African foragers and pastoralists. Proc. R. Soc. B Biol. Sci. 276, 347–354. https://doi.org/10.1098/rspb.2008.1028.

Nandy, S., Irving, M., Gordon, D., Subramanian, S.V., Smith, G.D., 2005. Poverty, child undernutrition and morbidity: new evidence from India. Bull. World Health Organ. 83, 210–216.

de Onis, M., Onyango, A.W., Borghi, E., Nishida, C., Siekmann, J., 2007. Development of a WHO growth reference for school-aged children and adolescents. Bull. World Health Organ. 85, 660–667.

Reed, W.L., Clark, M.E., Parker, P.G., Raouf, S.A., Arguedas, N., Monk, D.S., Snajdr, E., Nolan Jr., V., Ketterson, E.D., 2006. Physiological effects on demography: a long-term experimental study of testosterone's effects on fitness. Am. Nat. 167, 667–683. https://doi.org/10.1086/503054.

Rilling, J.K., 2013. The neural and hormonal bases of human parental care. Neuropsychologia 51, 731–747.

Robinson, C., Schumacker, R.E., 2009. Interaction effects: centering, variance inflation factor, and interpretation issues. Mult. Linear Regression Viewpoints 35, 6–11.

Ronay, R., von Hippel, W., 2010. The presence of an attractive woman elevates testosterone and physical risk taking in young men. Soc. Psychol. Personal. Sci. 1, 57–64. https://doi.org/10.1177/1948550609352807.

Rosenbaum, S., Gettler, L.T., 2018. With a little help from her friends (and family) part II: non-maternal caregiving behavior and physiology in mammals. Physiol. Behav. 193, 12–24. https://doi.org/10.1016/j.physbeh.2017.12.027.

von Rueden, C.R., Jaeggi, A.V., 2016. Men's status and reproductive success in 33 non-industrial societies: effects of subsistence, marriage system, and reproductive strategy. Proc. Natl. Acad. Sci. 113, 10824–10829. https://doi.org/10.1073/pnas.1606800113.

von Rueden, C., Gurven, M., Kaplan, H., 2008. The multiple dimensions of male social status in an Amazonian society. Evol. Hum. Behav. 29, 402–415. https://doi.org/10.1016/j.evolhumbehav.2008.05.001.

Saltzman, W., Ziegler, T.E., 2014. Functional significance of hormonal changes in mammalian fathers. J. Neuroendocrinol. 26, 685–696. https://doi.org/10.1111/jne.12176.

Saxbe, D.E., Schetter, C.D., Simon, C.D., Adam, E.K., Shalowitz, M.U., 2017. High paternal testosterone may protect against postpartum depressive symptoms in fathers, but confer risk to mothers and children. Horm. Behav. 95, 103–112. https://doi.org/10.1016/j.yhbeh.2017.07.014.

Smith, E.A., 2004. Why do good hunters have higher reproductive success? Hum. Nat. 15, 343–364. https://doi.org/10.1007/s12110-004-1013-9.

Smuts, B.B., Gubernick, D.J., 1992. Male-infant relationships in nonhuman primates: paternal investment of mating effort? In: Hewlett, B.S. (Ed.), Father-child Relationships: Cultural and Biosocial Contexts. Aldine de Gruyter, New York, pp. 1–29.

Stanton, S.J., Liening, S.H., Schultheiss, O.C., 2011. Testosterone is positively associated with risk taking in the Iowa gambling task. Horm. Behav. 59, 252–256. https://doi.org/10.1016/j.yhbeh.2010.12.003.

Storey, A.E., Ziegler, T.E., 2016. Primate paternal care: interactions between biology and social experience. Horm. Behav. 77, 260–271. https://doi.org/10.1016/j.yhbeh.2015.07.024.

Storey, A.E., Delahunty, K.M., McKay, D.W., Walsh, C.J., Wilhelm, S.I., 2006. Social and hormonal bases of individual differences in the parental behaviour of birds and mammals. Can. J. Exp. Psychol. 60, 237–245.

Trainor, B.C., Marler, C.A., 2001. Testosterone, paternal behavior, and aggression in the monogamous California mouse (*Peromyscus californicus*). Horm. Behav. 40, 32–42. https://doi.org/10.1006/hbeh.2001.1652.

Trumble, B.C., Cummings, D.K., O'Connor, K.A., Holman, D.J., Smith, E.A., Kaplan, H.S., Gurven, M.D., 2013. Age-independent increases in male salivary testosterone during horticultural activity among Tsimane forager-farmers. Evol. Hum. Behav. 34, 350–357. https://doi.org/10.1016/j.evolhumbehav.2013.06.002.

Trumble, B.C., Smith, E.A., O'Connor, K.A., Kaplan, H.S., Gurven, M.D., 2014. Successful hunting increases testosterone and cortisol in a subsistence population. Proc. Biol. Sci. 281, 1–8.

Weisman, O., Zagoory-Sharon, O., Feldman, R., 2014. Oxytocin administration, salivary testosterone, and father–infant social behavior. Prog. Neuro-Psychopharmacol. Biol. Psychiatry 49, 47–52. https://doi.org/10.1016/j.pnpbp.2013.11.006.

Wells, J.C.K., Hallal, P.C., Wright, A., Singhal, A., Victora, C.G., 2005. Fetal, infant and childhood growth: relationships with body composition in Brazilian boys aged 9 years. Int. J. Obes. 29, 1192–1198. https://doi.org/10.1038/sj.ijo.0803054.

WHO Multicentre Growth Reference Study Group, 2006. WHO Child Growth Standards: Length/Height-for-age, Weight-for-age, Weight-for-length, Weight-for-height and Body Mass Index-for-age: Methods and Development.

Wingfield, J.C., Hegner, R.E., Dufty, A.M., Ball, G.F., 1990. The “challenge hypothesis”: theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. Am. Nat. 136, 829–846. https://doi.org/10.1086/285134.

Winking, J., Koster, J., 2015. The fitness effects of men's family investments: a test of three pathways in a single population. Hum. Nat. 26, 292–312. https://doi.org/10.1007/s12110-015-9237-4.