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Marital status and sleeping arrangements predict salivary testosterone levels in rural Gambian men

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Acknowledgements

We are extremely grateful to the people of Keneba and Manduar for participating in our study. We also thank our field assistant and translator, Momodou Darboe, Gillian Bentley for loaning anthropometric equipment, Kesson Magid for advice on our study design, and Jonathan Wells for advice and practical assistance in the field. This project was supported by a British Academy Grant to Rebecca Sear (Grant #: SG-52128); a UK Medical Research Council (MRC) / Economic and Social Research postdoctoral fellowship to Alejandra Núñez-de la Mora (Grant#: PTA-037-27-0135); and the MRC & the Department for International Development (DFID) under the MRC/DFID Concordat agreement (MRC Programmes: MC-A760-5QX00).

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Abstract:

Variation in male testosterone has been hypothesized to reflect the evolved hormonal regulation of investment in mating versus parenting effort. Supporting this hypothesis, numerous studies have observed lower testosterone in married men and fathers compared with unpartnered and childless men, consistent with relatively elevated resource allocation to parenting as opposed to mating effort. Furthermore, lower testosterone has been reported among fathers more actively engaged in direct caregiving. However, it remains unclear whether these findings generalize cross-culturally. Most studies have been conducted in relatively urban, affluent, and low fertility settings where marriage is predominantly monogamous. We contribute new data on testosterone variation in 100 rural Gambian men from a polygynous, high fertility population, where cultural norms dictate that marriage and fatherhood occur in close succession. Married men (almost exclusively fathers) had lower average morning salivary testosterone than unmarried men (almost exclusively childless). This difference, however, could not be statistically differentiated from declines in testosterone observed with age. Independently of age differences and other potential confounds, we find that (i) among married men, polygynously married men had higher afternoon testosterone than monogamously married men; and (ii) fathers who sleep in the same room as their children had lower morning and afternoon testosterone than those who sleep apart from their children. We also document that body mass index was positively associated with afternoon testosterone. These findings, from a novel setting, provide additional support for the hypothesis that testosterone regulates human paternal care.

Keywords: Testosterone, Polygyny, Fatherhood, Paternal Care, Gambia.

1. INTRODUCTION

Evolutionary life history theory posits a fundamental resource allocation trade-off between mating effort (resources invested in competing for mates) and parenting effort (resources invested in rearing offspring). A substantial body of evidence has been amassed to support the existence of this trade-off across the animal kingdom (Stiver & Alzono 2009). Recent studies also highlight that a trade-off between mating and parenting effort is not always inevitable, in part, because behaviors that promote mating success may also have positive impacts for offspring in some circumstances (Stiver & Alzono 2009). Where trade-offs do exist, testosterone production has been identified as a potential mediator of the 'decision' to allocate resources to mating effort vs. parenting effort (Wingfield et al. 1990). Testosterone is an androgenic steroid hormone supporting many aspects of male mating effort, including factors such the development and maintenance of sexual dimorphic musculature and bone structure, libido, courtship and conspecific aggression (Archer, 2006; Bribiescas, Ellison, & Gray, 2012).

In many studies, across a range of both avian and mammalian taxa, males have been shown to have relatively high testosterone when engaging in mating effort, and relatively low testosterone when partnered with females and/or when cooperating with them to raise young (Magrath & Komdeur, 2003). Negative associations between testosterone and paternal care have been most commonly observed where parental care is direct, i.e. including conspicuous parenting behaviors such as incubation, infant carrying and provisioning (reviewed in Onyango, Gesquiere, Altmann & Alberts, 2013). However, positive associations between testosterone and paternal care have also been observed, perhaps reflecting instances where care includes more indirect paternal behaviors such as aggressive defense of offspring (Onyango, Gesquiere, Altmann, & Alberts, 2013).

Human paternal investment, while often substantial in relation to other mammals, is facultative, rather than obligatory, and the anthropological record indicates considerable cross-cultural variability in both how fathers invest, and how much they invest, in their children (Shwalb, Shwalb & Lamb 2013; Gray & Anderson 2010; Lamb 2004; Marlowe 2000). Despite this variation, most research on testosterone and its relationship to indicators of male mating or parenting effort has been carried out within only a narrow sliver of our socioecological range (Gray & Campbell 2009). The majority of studies are based on relatively urbanized, wealthy and healthy populations where monogamous marriage and some degree of direct paternal care are the norm. In these settings, testosterone has been reported to be negatively associated with marriage and fatherhood (e.g. Gray, Yang, & Pope, 2006; Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002). However, such studies have often relied on cross-sectional between-subject designs, raising important concerns about causality. Cross-sectional studies, for example, cannot distinguish whether fatherhood suppresses testosterone or if men with lower testosterone are more likely to become fathers. Addressing this concern, Gettler et al. (2011) used a large longitudinal sample from Cebu City, in the Philippines (over 600 participants) to demonstrate that (i) men with higher testosterone are more likely to marry than men with lower testosterone; (ii) men who marry and become fathers experience greater declines in testosterone compared to those than remain unmarried; and (iii) men who spend more time engaged in child care have lower testosterone levels than fathers who provide less care. More recently, Holmboe et al. (2017) report that in a longitudinal sample of over 1000 Danish men sampled over a

10-year period, that (i) men who went from unmarried to married during the study period experienced an accelerated age-related decline in testosterone, while (ii) men who went from married to unmarried experienced an attenuated age-related decline. These findings are consistent with the view that testosterone mediates trade-offs between mating and parenting effort in humans.

A small number of (cross-sectional) studies from less affluent and more diverse socioecological settings indicate that the association between testosterone and indicators of paternal care in humans such as marriage and fatherhood may be context dependent, with results from such settings tending to be less clear-cut and less consistent (reviewed in Gettler, 2016; Gray, McHale & Carre, in press). For example, Muller et al. (2009) documented a negative relationship between a man's residence with children aged 10 years or younger and testosterone among the Tanzanian Hadza, but not among the neighboring Datoga. Furthermore, among the Hadza, but not the Datoga, the age of the man's youngest child was negatively and significantly correlated with a man's daily change in testosterone between morning and evening. Muller and colleagues (2009) argue that these differences reflect the fact that direct paternal care is typically lower in pastoralist populations like the Datoga compared to foragers like the Hadza. If this line of reasoning is correct, then pair-bonding is not a universal correlate of testosterone reduction in humans. Rather testosterone declines only in socioecological contexts where union formation is typically followed by relatively high investments in direct paternal care.

The incidence of polygynous marriage may also be responsible for variation in patterns of testosterone variation between different socioecological settings. However, the small literature on this topic has led to varying predictions and mixed results. Testosterone has been predicted to be both higher and lower in polygynous, compared to monogamous, men, and has been empirically observed to be either higher, lower or statistically indistinguishable in polygynously married, compared to monogamously married, men. In the first study to consider polygynous marriage, Gray (2003) predicted that testosterone would be *lower* in polygynously married men compared to monogamously married men among the Kenyan Swahili, because, on average, polygynously married men had more offspring and showed less interest in obtaining another wife than monogamously married men (indicating lower mating effort). However, polygynously married men had higher afternoon and evening testosterone levels in this population. Gray (2003) speculates three potential explanations for this result. First, polygynous men may have higher testosterone because of greater requirements in mating effort in the form of mate guarding behavior. Second, higher testosterone production may be required for a (presumed) greater frequency of sexual intercourse for polygynously married men. Third, if healthier men are more likely to have high testosterone and also have more success on the mating market, then polygynous marriage will be associated with higher testosterone independently of a man's strategic investment in mating vs. parenting effort. However, contrary to this explanation, men in polygynous marriages were not taller (indicating better physical health, at least in childhood) than other men.

In a later study of Kenyan Ariaal pastoralists, Gray et al. (2007) reported lower morning testosterone levels in partnered men compared to unpartnered men, but found no overall difference in testosterone between polygynous and monogamously married men. Men over 40 years of age did however have lower testosterone when polygynously married. The authors suggest that this may be because in this context polygynous marriage is better predicted by age-related variation in wealth, rather than behaviors facilitated via testosterone production. Following the work of Gray, Alvergne et al. (2009) predicted *higher* testosterone in polygynously married men compared to monogamously married men (the opposite of Gray's initial prediction, but consistent with the results of Gray 2003) on the basis that polygynous marriage indicates assumed higher mating effort. Supporting this prediction, in a population of agriculturalists from rural Senegal, they report that among men under 50, polygynously married men had higher morning testosterone levels than monogamous men. They also report that married fathers had lower testosterone levels than unmarried non-fathers overall. Finally, Muller et al. (2009) reported no difference in the testosterone levels of polygynously married versus monogamously married Datoga men in Tanzania.

The studies reviewed above provide valuable insights, but more cross-cultural data is clearly required to determine the generality of hormonal regulation of human paternal care. In this paper, we present data on testosterone's relationship with marital status and fatherhood from a highly polygynous, high fertility population in rural Gambia. Following the literature described above, we hypothesize that testosterone will be lower for married fathers compared to unmarried non-fathers, reflecting the reallocation of resources from mating to parenting effort. Furthermore, we examine whether testosterone production varies between monogamously and polygynously married men. Following the mixed predictions and past results on this topic described above, our consideration of this contrast is exploratory rather than predictive. We further explore whether or not additional factors relating to parenting and relationship status are associated with testosterone levels, including the age and number of children, and whether or not fathers report sleeping in the same room as their children. It is hypothesized that having more and younger children, and co-sleeping with children are an indication of greater resource allocation to paternal care and thus will be associated with lower testosterone. In all contrasts, we also consider the potential confounding effects of differences in testosterone associated with male age, health and wealth. As such our study further provides valuable data on the sociodemographic and socioeconomic correlates of testosterone variation in less affluent, rural developing populations.

2. DATA AND METHODS

2.1 Study Site and Sampling

All field research was conducted between July to August 2010 in and around the Medical Research Council (MRC) Unit The Gambia's rural field station in the village of Keneba, in the Kiang West region of The Gambia. Field work was carried out by David Lawson and Rebecca Sear, together with field staff from MRC Keneba. Data collection took place during the wet season, when all adults are traditionally engaged in farming activities. Informed consent was obtained from all participants and community support was sought through meetings with village elders and school head teachers. All individual data were anonymized before analysis. Ethical approval for the study was granted by the joint Gambian Government / MRC Unit The Gambia's Ethics Committee.

The MRC has had a presence in the area for over 60 years, and has a long history of providing medical care to the local population as well as carrying out a strong nutrition-related science program (McGregor 1991; Hennig et al. 2015). Early studies of this site characterize the population as experiencing sub-optimal growth and a high burden of infectious disease (McGregor & Smith 1952). While the services of the MRC are likely to have improved health conditions for many, the population nevertheless can be categorized as experiencing relative undernutrition and ill health compared to study populations from more affluent low fertility, low mortality settings. With the majority of men of all ages involved in farm work, energetic expenditure can also be characterized as relatively high.

One hundred men were recruited for the study. The final sample includes 69 men in Keneba village itself and 31 men from the neighboring village of Manduar (around 10 minutes by motorbike from Keneba). The sampling of men was assisted through use of the demographic surveillance records (as part of the West Kiang Demographic Surveillance System), which was used to draw up a list of unmarried, monogamously and polygynously married men between the ages of 20 and 70 years from each village. Men on this list where then sampled based on immediate availability to participate in order to maximize opportunities for data collection during a field season of six weeks. Households were visited around sunrise for subject recruitment. Once participant recruitment slowed in Keneba, recruitment shifted to Manduar, where data collection was terminated at the end of the field season. As sampling was opportunistic it cannot be treated as a representative sample of villagers. Nevertheless, effort was made to achieve a sample spanning all age groups and to include men representative of the local population.

The large majority of participants (85%) identified as Mandinka, but a number of other ethnic affiliations where also recorded, including Fula and Jola. The region is predominantly patrilineal, patrilocal and of Muslim faith. Polygynous marriage is common, with a maximum of four wives in line with teaching of Islam. Divorce occurs occasionally, and women typically remarry relatively quickly after widowhood (sometimes practicing the levirate) or divorce. As is common in polygynous societies, marriage and first birth tends to occur much earlier for women than men. Fertility is still relatively high in this population, but has seen a sharp decline over the past few decades in the villages sampled here, thanks to medical care provided by the MRC, and is somewhat lower than for the Gambia as a whole (Rayco-Solon 2004). Small-scale subsistence agriculture is the main livelihood in both Keneba and Manduar, however small business ownership and supplementary income from wage labor is not uncommon, particularly in Keneba including work in service of the MRC field station, e.g. working as MRC handymen, security guards, gardeners and mechanics.

2.2 Testosterone Sampling

Each participant provided two daily salivary samples over two non-consecutive days (a total of 4 samples). Morning samples were taken shortly after waking, and afternoon samples taken after four pm and before sunset. Men were asked not to eat anything before salivary samples were collected in the morning and at least an hour after the last evening meal, and to refrain from consuming kola nut on the sampling day. Saliva samples were labeled and immediately placed in a portable freezer bag upon collection, then transferred to a freezer at the MRC Keneba field station within hours of collection. At the end of the data collection, frozen samples were shipped on dry ice to the Endocrinology and Ecology Laboratory at the Wolfson Research Institute for Health and Wellbeing, Durham University, United Kingdom for analysis.

Salivary testosterone levels were determined by Enzyme Immunoassay (EIA) method, using SALIMETRICS Salivary Testosterone kits (Salimetrics Europe, UK). Saliva samples were defrosted at room temperature on day of assay. Once thawed, samples were vortexed and spun at 3200 rpm at 4°C for 15 min in a refrigerated centrifuge (ThermoScientific CL30R). Reagents and serial dilutions of the testosterone standard were prepared as per kit instructions. 25 μL of standards, controls, and unknowns were pipetted in duplicate into appropriate wells across a 96 well microtiter plate. The microtiter plate was mixed on a plate shaker for 5 minutes at 500 rpm and incubated at room temperature for an additional 55 minutes. The microtiter plate was washed 4 times with 1X wash buffer on a microplate washer. The plate was incubated on a plate shaker for 5 minutes at 500 rpm and incubated in the dark at room temperature for an additional 25 minutes. 50 μL of stop solution were added and the plate mixed on a plate shaker for a further 3 minutes at 500 rpm until all wells turned yellow. The plate was read in a micro plate reader (Biotek ELx808) at 450 nm. Final salivary testosterone concentrations were calculated using Gen 5 Software Version 1.06.1. The sensitivity of this assay is 1 pg/ml. The four saliva samples of each participant were always assayed within the same plate. The mean intra-assay CV was 8.2% and the mean inter-assay CVs were 10.5% for low controls and 8.3% for high controls.

Two metrics were then derived as outcome variables for the analysis of testosterone data for the 100 sampled men: (i) *average morning testosterone*, i.e. average of the two morning samples and (ii) *average evening testosterone*, i.e. average of the two afternoon samples. Morning levels are considered to reflect endogenous physiological differences in testosterone, while afternoon levels are believed to be more indicative of short-term ecological and behavioral effects (Gray et al., 2007).

2.3 Anthropometric Data and Participant Survey

Anthropometric measurements were obtained from all men, including standing height, weight and tricep skinfold thickness. For weight and height measurements, men removed shoes and any items from their pockets, but were measured in light clothing because private space was not always available. Skinfold measurements were made shirtless or under lifted clothing. Height and weight measurements were taken twice, and skinfolds taken three times before being averaged and entered into the database. Body mass index (BMI) was calculated as the ratio of weight (kg)/height (m^2). Height was recorded to the nearest millimeter and weight to the nearest 100 grams. All measurements were taken by the same individual to minimize inter-observer bias. In addition to saliva samples and anthropometric measurements, all men answered a short questionnaire to provide data on the participant's current marital status, reproductive history and current sleeping arrangements. Socioeconomic status was also measured by two variables. First, they stated whether or not they had received any wage-income within the last year. Second, participants subjectively rated their socioeconomic position relative to other households in their resident village choosing between four categories "Struggling", "Just about OK". "Comfortable" and "Well Off". All questionnaires were conducted by a field assistant fluent in Mandinka and local to West Kiang. Responses where immediately translated into English and transcribed, before being entered into a database for analysis.

2.4 Analysis Strategy

We first provide descriptive summaries of all independent variables by marital and fatherhood status, to better understand the key relevant differences between men in our study population. We then compute correlations between testosterone measures using the non-parametric Spearman's rank correlation test. After these steps, we investigate the effects of independent variables on testosterone levels using general linear regression. We first investigate the effects of potential confounds (i.e. age, anthropometric measurements, household wealth and village of residence) on each testosterone measure. Replicating Alvergne et al.'s (2009) analytical strategy, only the variables that were significant in this exploratory analysis where then carried forward as potential confounds in later models. After this step we contrast men by marital and fatherhood status presenting estimates first unadjusted for other variables, and then including controls for any potential confounds. Finally, we run contrasts among married fathers, considering whether testosterone levels vary by our additional measures of parenting and relationship status. All analyses were carried out using the software IBM SPSS v.24.

3. RESULTS

3.1 Descriptive Summary by Marital and Fatherhood Status

Out of the 100 sampled men, 19% were currently unmarried, 52% monogamously married and 29% polygynously married. Among polygynous men, 72% (21/29) had two wives and 28% (8/29) had three wives. Almost all of the unmarried men reported that they were childless, while 96% (50/52) and 100% of monogamously married and polygynously married men had fathered children respectively. This close association between marriage and fatherhood is to be expected in this cultural setting, and is probably reflective of much of human history. Given this structure of the data, we are unable to statistically distinguish the effects of marriage and fatherhood in this population.

Descriptive statistics (**Table 1**) reveal that unmarried men were typically younger than married men, and polygynously married men were older than monogamously married men. Anthropometric measurements indicate little difference in height by marital status. However, married men had higher BMI than unmarried men. The mean height of men was 170.9cm (standard deviation 6.6) and the mean BMI was 21.7 (standard deviation 3.7). This compares to a mean height of 168cm and mean BMI 20.4 for adult men in this population between 1950-1980 (Sear 2006), suggesting recent modest improvements in general health. Tricep skinfolds were lowest in unmarried men and highest in polygynously married men. In terms of socioeconomic indicators, compared to others in their village polygynously married men were the most likely to report being relatively "comfortable" or "well-off", and unmarried men most likely to report being "struggling" or "just about OK". Some form of wage labor in the last year was most common in polygynous men and least common in unmarried men. The mean number of living children was 4.5 for monogamously married men and 11.1 for polygynously married men. Data on the age of the youngest child was available for 75/80 men who reported having children, with a mean of 33.0 months (standard deviation: 44.7 months). Polygynously married men were more likely to have a younger child compared to monogamously married men.

Just under half (42%) of monogamously married men reported generally sleeping in the same room as their children, while 15% of polygynously married men did. Half

(50%) of monogamously married men and 19% of polygynously married men reported that they typically slept in the same room as their wife. Men who slept in the same room as their children also typically slept in the same room with their wife. As such, in the analyses which follow, we contrast men on the basis of sleeping in the same room or not as their children, acknowledging that this normally implies sleeping in the company of both their wife and children, rather than in the company of children alone. Variation in sleeping arrangements is not surprising in this context, with multiple factors likely to influence its occurrence. Traditionally it was common for newly married wives to remain living with their parents until after the birth of the first child or two, however it is unclear whether this custom is currently maintained. Once living together, separate rooms/structure for each wife may be available upon marriage within the patrilineal compound. However, some men lack this resource, including those that have migrated into the village or for those that opt to begin a new compound, so that opportunities to sleep separately will be dependent on resources to build and maintain separate rooms/structures for each wife. In addition to these factors, variation in cultural norms (e.g. between ethnic groups) and individual preference are also likely to be significant determinants.

3.2. Testosterone Variation and Influence of Potential Confounds

Four testosterone samples from four different men were excluded from analysis due to contamination by traces of blood in their saliva, leaving 396 valid testosterone samples. Average morning testosterone and average afternoon testosterone were only calculated for the remaining valid 3 samples for the four men affected. Although participant compliance with sampling protocol was believed to be high, in two morning and 13 evening samples it was noted that saliva was stained, consistent with the recent consumption of kola nut. Based on results of a previous study in a betel nut chewing population that found no significant interference of this practice on salivary testosterone levels up to 4h after consumption (Magid, 2011), the decision was made to include all samples in our analysis.

Average morning testosterone levels ranged from 40.3 to 299.4 pg/ml (mean: 113.0; standard deviation: 42.9) and average afternoon testosterone levels ranged from 32.3 to 196.92 (mean: 86.11; standard deviation 30.11). During the day, between morning and afternoon samples, testosterone levels declined by a mean of 16.5% (standard deviation: 29.2%). Morning testosterone was positively correlated with afternoon testosterone (spearman's correlation test, $\rho=0.46$, $p<0.001$).

Multivariate regression models predicting testosterone levels which included age, anthropometric and socioeconomic variables and village of residence as independent variables reveals a number of statistically significant relationships (**Table 2**). Older men had both lower average morning and afternoon testosterone (**Figure 1**). Of the anthropometric variables, BMI was the only measure to be significantly correlated with testosterone: men with higher BMI had higher afternoon testosterone, but not morning testosterone (**Figure 1**). Consequently, men with a higher BMI typically experienced less decline in testosterone throughout the day. Height and tricep skinfold measurements were not associated with any testosterone measure. Men who had wage income had higher afternoon testosterone than those without wage income. Men who assessed their own current financial situation as "comfortable" as opposed to "struggling" or "just about ok" had lower morning testosterone. Over and above these relationships, residing in Mandaur village was predictive of a lower morning testosterone and higher afternoon testosterone. On the basis of this analysis we carry forward age, BMI, wage income, current financial status and village as potential confounds in multivariate models.

3.3. Comparison of Testosterone Levels by Marital and Fatherhood Status

In unadjusted models, married men had lower average morning testosterone. However, this difference was not independent of potential confounds (**Figure 2, Table 3**). Specifically, differences in average morning testosterone between unmarried and married men are statistically indistinguishable from age related declines in testosterone. Almost all men under 30 years of age are unmarried and almost all men over the age of the 30 are in monogamous or polygynous marriages (**Figure 1**). It is thus not possible to determine whether or not the observed pattern is best explained by differences in marital status or age.

3.4 Comparison of Testosterone Levels Among Married Men

We compared testosterone levels among married men by marriage type (monogamous or polygynous), the number of living children, the age of the youngest child and whether or not the father reported sleeping the same room as his children. For each of these contrasts a separate regression model was run (since these variables may be correlated and cell counts are small) which included adjustment for age, BMI, wage income, current financial status and village. Polygynously married men had higher afternoon testosterone than monogamously married men (**Figure 3, Table 4**). Furthermore, fathers who reported sleeping in the same room as their children had lower morning testosterone levels and afternoon testosterone levels compared to fathers who did not sleep in the same room (**Figure 4, Table 4)**. The number of living children and the age of the youngest child were not significant predictors of testosterone (**Table 4**).

4. DISCUSSION

4.1 Testosterone and Marital Status in rural Gambia

This study investigated testosterone variation and its relationship to indicators of mating and parenting effort in a highly polygynous and high fertility population in rural Gambia. The population is characterized by predominant reliance on small-scale agriculture. These features make the presented data relatively novel in the context of extant studies of testosterone, marriage and fatherhood, which have typically been conducted in more affluent settings and where monogamous marriage is the norm. We find that married men (almost exclusively fathers) had lower morning testosterone than unmarried men (almost exclusively childless). However, strong cultural norms related to age at first marriage mean that almost no men under the age of the 30 are married, while few men over this age are unmarried (**Figure 1**). These features of our data make it challenging to statistically distinguish effects of marriage, fatherhood and age-related declines in testosterone. As such we cannot rule out the possibility that observed differences in testosterone between married and unmarried men do not reflect resource allocation to mating vs. parenting effort, but are rather a by-product of age-declines in testosterone.

Muller et al. (2009) have hypothesized that testosterone will only decline at the onset of pair-bonding in contexts where relatively high direct paternal care is anticipated. Previous work using historical data form the current Gambian study population (i.e. 1950-1974) indicate that the presence of fathers is not essential for child survival, nor is it predictive of anthropometric indicators of children's nutritional status (Sear, Mace, & McGregor, 2000). Such findings might be interpreted as evidence that paternal care is relatively low in this context. Yet, the contributions of fathers may be obscured by studies correlating paternal absence with child outcomes if shortfalls in investment are made up by other kin when fathers are unavailable (see discussion in Lawson et al., in press). Consequently, the results of Sear et al. (2000) do not necessary imply paternal care is absent or inconsequential. We did not systematically collect data on paternal care in this study. However, direct paternal care was observed during data collection, with, for example, fathers being observed holding, feeding and bathing young children during participant interviews. As such we are skeptical that the failure to find a relationship between marriage/fatherhood and testosterone (independently from age) in this context can be accounted for by the absence of significant levels of paternal care.

Polygynously married men had higher levels of evening testosterone than monogamously married men. This is consistent with Gray (2003) and Alvergne et al. (2009) who also found that polygynously married men had higher testosterone than monogamously married men in samples from rural Kenya and Senegal respectively. However, Gray et al. (2007) and Muller et al. (2009) found no differences in testosterone between polygynously married and monogamously married men in the Kenya Ariaal and Tanzanian Datoga respectively. How best can we interpret this mixed pattern of results? As we outlined in our introduction, it is possible to predict higher or lower allocation of resource to mating effort for polygynously married men. On the one hand, polygynously married men may invest more in mating effort in order to sustain current marriages and engage in mate guarding behavior. On the other hand, monogamously married men may invest more in mating effort, since such men may have a good, or higher, chance of attracting a second wife than polygynous men have of attracting a third or fourth wife.

Which prediction is borne out in any particular population may depend on socioecologically variable factors such as the degree of polygyny, degree of reproductive skew, and level and type of paternal investment required. For example, in highly polygynous or highly reproductively-skewed populations, it may benefit polygynously married men to continue to invest in mating effort since they have a reasonably good chance of acquiring more wives; whereas in mildly polygynous populations, where acquiring more than two wives is rare, and/or where direct paternal investment is common, polygynous men may have little chance of acquiring more wives, and may need to focus their efforts on paternal investment instead. It is also possible that men with relatively high testosterone are selected into polygynous marriages. As such, the monogamous men category will include some men of relatively low mate value who will always remain monogamous men, which may drag down overall testosterone levels in the monogamous group. Descriptive data suggest that polygynously married men are typically healthier (have higher BMI) than monogamously married men, and that healthier men have higher testosterone. Our contrasts are independent of these differences. Nevertheless, residual confounding is possible and more data is needed to distinguish between these possibilities, including: longitudinal analysis to investigate changes in testosterone after partnership or parenthood, to help determine whether differences between polygynous and monogamous men are confounded by heterogeneity between men in mate value; and data from a wider range of populations to determine whether environmental factors might influence these relationships.

4.2 Testosterone and Co-sleeping

Sleeping in proximity to young children was predictive of relatively low morning and afternoon testosterone, consistent with our prediction, though number of children and age of youngest child were not associated with testosterone. A number of recent studies suggest that crude correlations between marital or paternal status and testosterone may not always be sufficient to pick up on associations between testosterone and indicators of mating and paternal effort, because of the diversity of mating and paternal behaviors in our species. Some studies, including those which do not show overall associations between testosterone and marital status of fatherhood, nevertheless show that more nuanced indicators, such as relationship quality between spouses (Gray et al. 2017), co-sleeping with children (Gettler et al. 2012), or an increase in the amount of paternal care fathers do (Gettler et al. 2015), are associated with testosterone in the predicted direction. Given the complexity of mating and parenting in our species, Gettler (2016) has proposed an integrative model for understanding paternal behavior, which incorporates an evolutionary, life-history theory perspective on how men should allocate resources between competing functions, but also takes into account environmental and cultural factors, and developmental processes, which influence men’s mating and parenting behavior. Such integrative models offer the best hope for understanding paternal behavior.

4.3 Testosterone, age, health and wealth

As well as correlations with relationship variables, we also observed: a negative association between testosterone and age; some evidence that higher BMI is associated with higher testosterone, and some evidence that testosterone is associated with socioeconomic status, though different socioeconomic measures showed different associations with testosterone.

It is possible that general declines in testosterone with age may in fact reflect the shift in resource allocation from mating effort to parenting effort across the life course as men shift from competing for mates to investing in offspring (see also Alvergne et al., 2009). If this is true, however, age-related declines in testosterone do not appear to be a universal feature of human endocrinology, with some but not all studies of non-western populations reporting lower testosterone levels in older men compared with younger men (Alvergne et al., 2009; Ellison et al. 2002). One study which explicitly compared the relationship between testosterone and age in different populations found that the age-related decline in well-nourished populations may be driven by particularly elevated testosterone in younger men, as the testosterone levels of older men were somewhat similar across populations (Ellison et al. 2002; see also Bribiescas 2006). The correlation between older age and lower testosterone we observe may reflect an age-related decline in testosterone, although it is difficult to exclude the possibility of cohort effects in this particular population. The decline in mortality in recent decades in this population may indicate an overall improvement in health in the population over time, perhaps leading to higher testosterone in younger cohorts. However, there is some evidence that improvements in child mortality were, initially at least, not necessarily accompanied by improvements in all aspects of child health: for example, while episodes of childhood diarrhea declined in the years after the establishment of the permanent medical clinic, child growth did not improve (Poskitt et al. 1999).

The mechanisms behind the associations observed between BMI and testosterone can also only be speculated on, given the paucity of data on such relationships from relatively low-resourced populations. BMI tends to be negatively correlated with testosterone in high income populations (MacDonald et al. 2010), and more detailed studies of body composition suggest that testosterone is negatively correlated with fat mass and positively correlated with lean mass (lending support to the argument that increased testosterone is linked to mating effort) (Vermeulen et al. 1999). In contrast, the study among the Ariaal of Kenya reported that testosterone was positively correlated with fat mass and not at all with lean mass (Campbell et al. 2003); and in Aché hunter-gatherers in Paraguay, a small positive association was seen between testosterone and BMI (Bribiescas 1996). These latter two populations are very lean compared with Western populations, as is this Gambian population, and these results raise the possibility that testosterone may show non-linear relationships with BMI or fat mass, with both men of low and high weight having lower testosterone than those of moderate weight or fat mass. These testosterone results also fit with a previous study in this population demonstrating that BMI is positively associated with both adult mortality and reproductive success (number of marriages, number of children and number of surviving children), whereas height was correlated with neither (Sear 2006). As with associations between age and testosterone, however, much more data from lower income populations is needed to determine exactly how and why testosterone may be associated with other physiological characteristics.

Finally, it is worth noting that the other physiological markers we obtained – height and skinfold thicknesses – were not correlated with testosterone (as was also observed in the Aché (Bribiescas 1996); see also Alvarado et al. (2015) for data from a well-nourished farming community where no musculature measures were associated with testosterone).

4.4 Methodological Considerations

The current study is limited by its reliance on cross-sectional data. Issues of close associations between marriage, fatherhood and age are typical of many 'traditional' populations, and longitudinal research will be likely be required to distinguish these factors in future analyses. Our sample size is comparable to past field studies of rural non-western populations, but is nevertheless small enough to limit statistical power in our analyses. It is also important that we consider whether our sample can be considered truly representative of the local population. One issue, likely also highly relevant to other contemporary rural populations, is that unmarried men may live away from their natal villages in pursuit of labor opportunities in more urban areas. It is interesting to speculate on whether such men may differ systematically from those who remain and where sampled in this study. If such men have higher testosterone levels, this could account for the failure of our study to find the predicted differences in testosterone between unmarried and married men (independently of age).

Our study revealed non-trivial differences in testosterone levels between the two study villages of Keneba and Manduar that remain over and above adjustment for the other variables considered in this study (**Tables 2** and **3**). It is unclear what accounts for this difference, but that such sizeable differences between adjacent villages exists suggests that we have much to learn about not only socioecological influences on male hormonal status beyond the effects of nutritional status, marriage and fatherhood. Keneba is a larger village with more cultural and socioeconomic influence from the researchers and visitors to the MRC base in this village than Manduar. It also has greater access the health clinic.

Finally, a confound making it potentially harder to detect marital and paternal influences on testosterone in this population compared to Western populations, is that patterns of social interaction can differ quite substantially between populations, beyond marriage patterns and paternal behaviour. For example, in Western populations, adults may have relatively little contact with children until they have their own. In higher fertility populations, such as the Gambia, adults may have far greater opportunities for interactions with children, even when unmarried and childless. If time spent with children is a proximate mechanism which reduces testosterone, then this could also even out differences in testosterone between unmarried, non-fathers and married fathers. Further, differences in patterns of social interactions during childhood and adolescence may also influence the development of these hormonal mechanisms and paternal behavior itself (Sear 2016; Sheppard, Garcia & Sear 2015).

4.5 Conclusion

We conclude that our findings provide additional, if tentative, support for the hypothesis that testosterone regulates human paternal care and mating effort. However, in agreement with Gettler (2016), we suggest that more direct measures of paternal care and mating effort should be prioritized in future studies, along with further longitudinal research on the development of human reproductive physiology, and of pair-bonding and paternal behavior more generally. It is of vital importance that such research is conducted outside of the contemporary western settings that currently dominate existing literature on testosterone variation. Such settings share a number of features uncharacteristic of our evolutionary past. Moreover, evolutionary ecology predicts significant environmental variation in adaptive responses, and strong cultural norms are observed surrounding, marriage, fatherhood and the ages and social contexts of life history transitions. A satisfying understanding of the role of testosterone in human behavioral variation can therefore only be achieved by increased commitments to cross-cultural research.

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Tables

Table 1: Descriptive Data on Fathers by Marital and Fatherhood Status

		Unmarried	Monogamously Married	Polygynously Married
Sample Size		19	52	29
Number of Wives	0	100%	-	-
	1	-	100%	-
	2	-	-	72%
	3	-	-	28%
Has Living children (% yes)		5%	96%	100%
Age in years		27.0 (12.8)	44.2 (10.6)	51.8 (9.2)
Height in cm		171.0 (7.3)	171.4 (7.23)	169.8 (4.7)
Body Mass Index		19.7 (3.0)	22.2 (4.0)	22.3 (3.4)
Tricep Skinfold in mm		6.5 (2.6)	8.8 (5.1)	10.8 (5.1)
Has Wage Income (% yes)		48%	73%	90%
Current Financial Situation	"Struggling or Just About OK"	58%	29%	17%
	"Comfortable"	37%	56%	62%
	"Well Off"	5%	15%	21%
Mean # of Living Children For Those With Children		-	4.5 (2.6)	11.1 (4.6)
Age of Youngest Child (months) For Those With Children		-	34.2 (31.3)	28.2 (44.1)
Age of Youngest Child	0-18 months	-	39%	56%
	19-72 months	-	50%	36%
	73+ months	-	11%	8%
Sleeps in same room as children (% yes)		-	42%	15%
Sleeps in same room as wife (% yes)		-	50%	19%
Average Morning Testosterone in pg/ml		134.4 (59.9)	110.7 (40.9)	103.2 (42.9)
Average Afternoon Testosterone in pg/ml		94.07 (27.6)	83.1 (27.2)	86.1 (30.1)

% for categorical; means and standard deviations in brackets for continuous variables.
Data is complete on all variables – except: "; "age of youngest child" is missing for 5/80 fathers; sleeps in same room as wife had missing data for 4 married men.

Table 2: Multivariate General Linear Regressions Predicting Testosterone Levels by Age, Health, Wealth and Village			
Outcome Variable		Average Morning Testosterone (pg/ml)	Average Afternoon Testosterone (pg/ml)
Statistic		Parameter Estimate β (± SE)	Parameter Estimate β (± SE)
Intercept		121.07 (± 111.57)	-4.15 (± 73.04)
Age *(years)*		**-1.29 (± 0.30) *****	**-0.81 (± 0.19) *****
Body Mass Index		1.61 (± 1.61)	**3.85 (± 1.06) ****
Height *(cm)*		0.14 (± 0.60)	0.18 (± 0.39)
Tricep Skinfold *(mm)*		-0.17 (± 1.23)	-0.60 (± 0.83)
Has Wage Income *(reference: no)*	Yes	11.00 (± 10.63)	**15.02 (± 6.96) ***
Current Financial Situation *(reference: "Struggling" or "Just About OK")*	"Comfortable"	**-17.81 (± 8.90) ***	-3.75 (± 5.89)
	"Well Off"	-12.14 (± 12.99)	-4.44 (± 8.50)
Village *(reference: Keneba)*	Manduar	**-18.49 (± 9.69) +**	**27.15 (± 6.34) *****
+ = p<0.1; * = p<0.05; ** = p<0.01; *** = p<0.001			

Table 3: Multivariate General Linear Regressions Predicting Testosterone Levels by Marital Status, With and Without Adjustment for Potential Confounds				
Outcome Variable			Average Morning Testosterone (pg/ml)	Average Afternoon Testosterone (pg/ml)
Statistic			Parameter Estimate β (± SE)	Parameter Estimate β (± SE)
Unadjusted Model	Intercept		**134.41 (± 9.59)*** **	**94.07 (± 6.89)+**
	Marital Status (reference: unmarried)	Married	**-26.42** ** (± 10.65)	-9.83 (± 7.65)
Adjusted Model	Intercept		**143.79 (± 26.50)*** **	**32.50 (± 17.95)+**
	Marital Status (reference: unmarried)	Married	-6.68 (± 13.15)	-4.95 (± 8.63)
	Age (years)		**-1.12 (± 0.34)** **	**-0.77 (± 0.23)** **
	Body Mass Index		1.57 (± 1.07)	**3.36 (± 0.71)*** **
	Has Wage Income (reference: no)	Yes	11.53 (± 10.60)	**14.91 (± 6.96)***
	Current Financial Situation *(reference: "Struggling" or "Just About OK")*	"Comfortable"	**-16.41 (± 8.94)+**	-2.00 (± 5.87)
		"Well Off"	-10.67 (± 13.09)	-3.16 (± 8.59)
	Village (reference: Keneba)	Manduar	**-18.48 (± 9.61)+**	**27.36 (± 6.31)*** **
+ = p<0.1; * = p<0.05; ** = p<0.01; *** = p<0.001				

Table 4: Multivariate General Linear Regressions Predicting Testosterone Outcome Variables Among Married Men by Marital Status, Co-sleeping, Age of Children and Number of Children			
Outcome Variable		Average Morning Testosterone (pg/ml)	Average Afternoon Testosterone (pg/ml)
Statistic		Parameter Estimate β (± SE)	Parameter Estimate β (± SE)
Marital Status (reference: Monogamous)	Polygynous	-1.54 (± 8.56)	**12.48 (± 6.21)***
Number of Wives (reference: 1)	2	-2.27 (± 9.20)	**14.38 (± 6.62)***
	3	-1.09 (± 14.25)	5.62 (± 10.24)
Father sleeps with children (reference: no)	yes	**-18.62 (± 8.50)***	**-11.17 (± 6.22)+**
Age of youngest children (months)	continuous	0.10 (± 0.10)	-0.02 (± 0.08)
Age of youngest child (reference: 0-18months)	19-72 months	2.45 (± 7.56)	-3.10 (± 6.11)
	73+ months	10.41 (± 13.65)	-4.62 (± 11.04)
Number of children	continuous	0.37 (± 1.07)	1.23 (± 0.81)
Number of children (reference: 1-4)	5-9	-5.22 (± 9.92)	7.37 (± 7.50)
	10+	3.30 (± 11.86)	**15.49 (± 8.96)+**

+ = p<0.1; * = p<0.05; ** = p<0.01; *** = p<0.001
Each row is a different model (i.e. each independent variable of interest is considered separately). Each model includes an intercept, age, BMI, wage income, current financial status and village (estimates not shown)

Figures

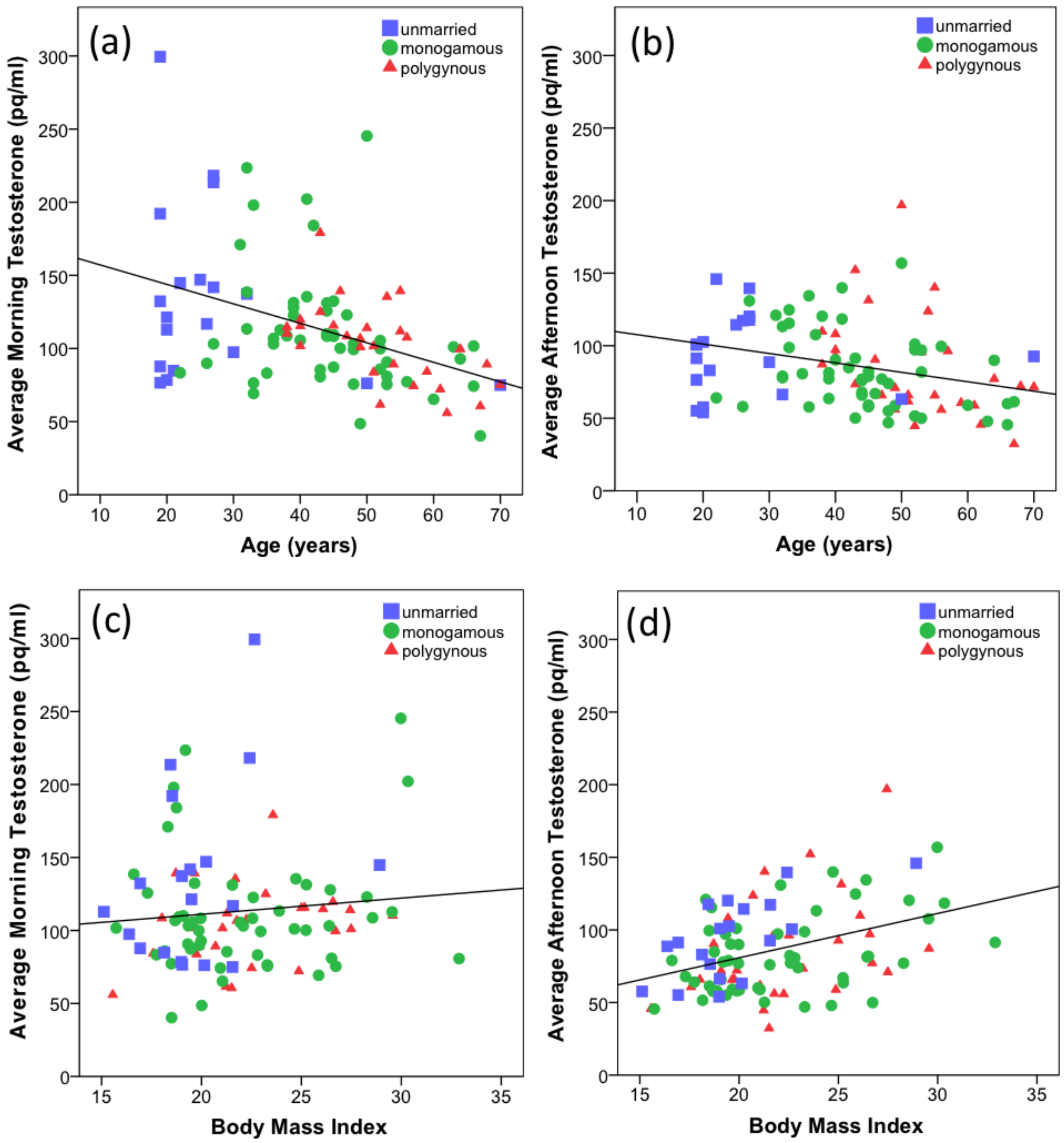

Figure 1: Scatterplots of Testosterone Variation by Age and Body Mass Index (n=100): Graphs present raw data coded by marital status. Age is positively associated with morning and afternoon testosterone (panels (a) and (b) respectively). These relationships are statistically significant in multivariate analysis (Table 2). BMI is also positively associated with morning and afternoon testosterone (panels (c) and (d) respectively), but only the latter association is statistically significant in multivariate analysis (Table 2).

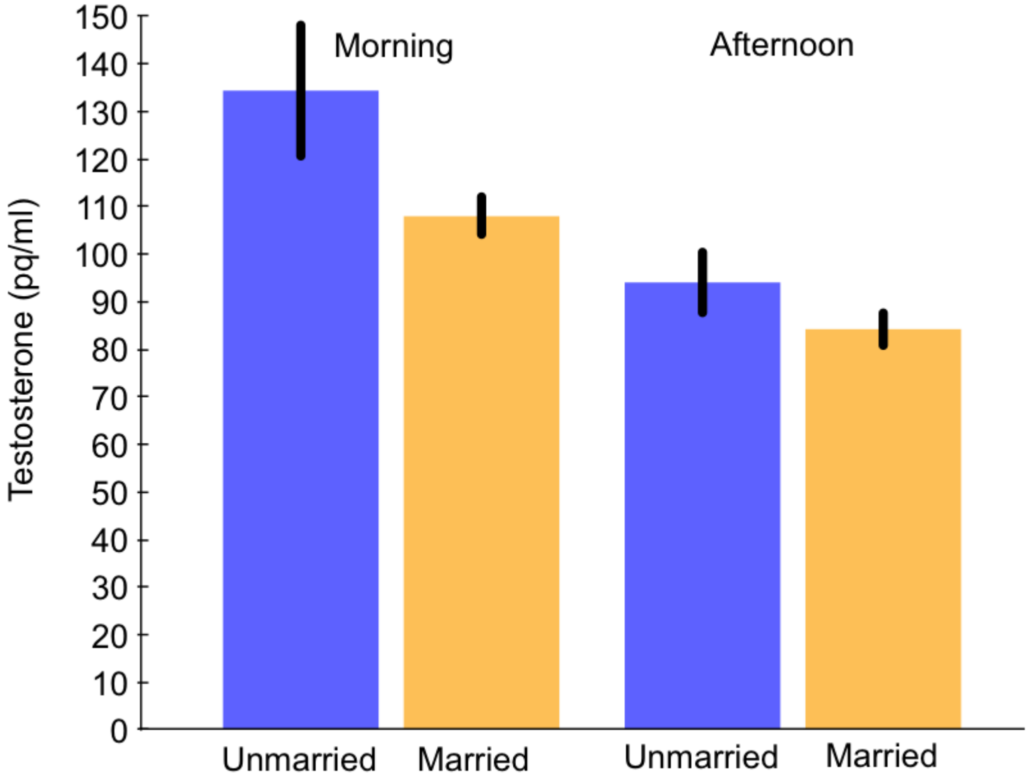

Figure 2: Average Morning and Afternoon Testosterone by Marital Status.

In unadjusted models, married men had significantly lower morning testosterone than unmarried men. However, in adjusted models there is no difference in testosterone levels by marital status (Table 3). The graph plots raw data, error bars represent ±SE. Unmarried men, n = 19; Married Men, n = 81.

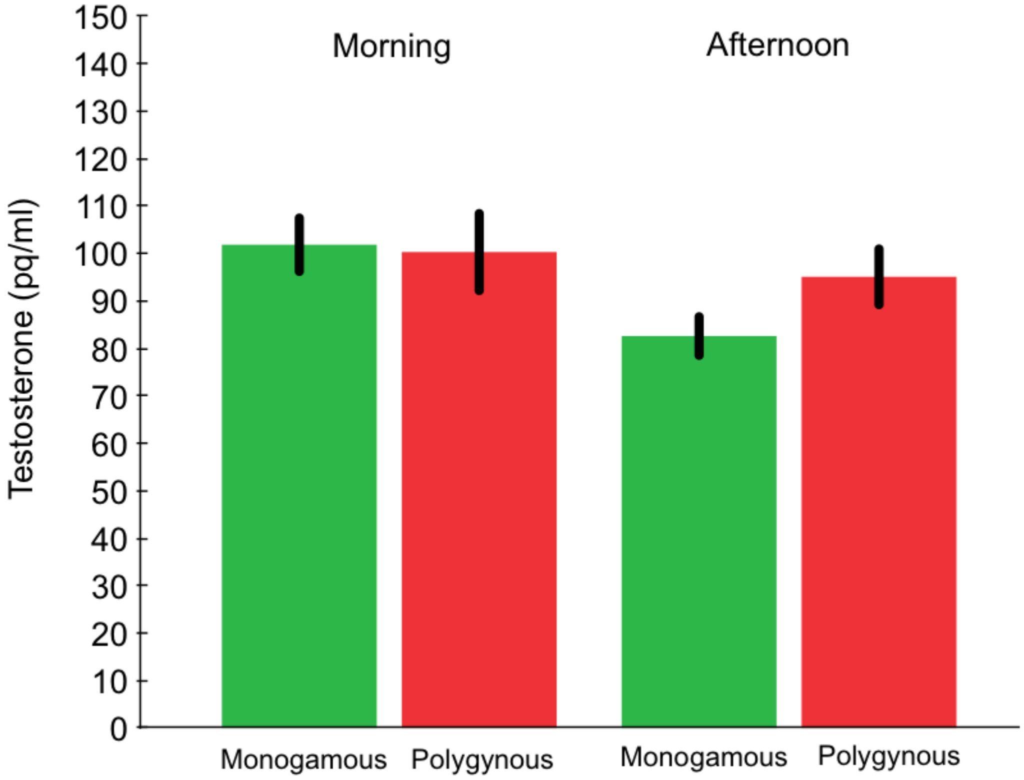

Figure 3: Estimated Marginal Means for Average Morning and Afternoon Testosterone by Monogamous vs. Polygynous Marriage

Polygynously married men had significantly higher afternoon testosterone than monogamously men, independently of age, BMI, wage income, current financial status and village of residence (Table 4). The graph plots estimated marginal means, assuming mean values for age and BMI, no wage income, “struggling” or “just about OK” current financial status and residence in Keneba village. Error bars represent ±SE. Monogamously men, n = 52; Polygynously Married Men, n = 29.

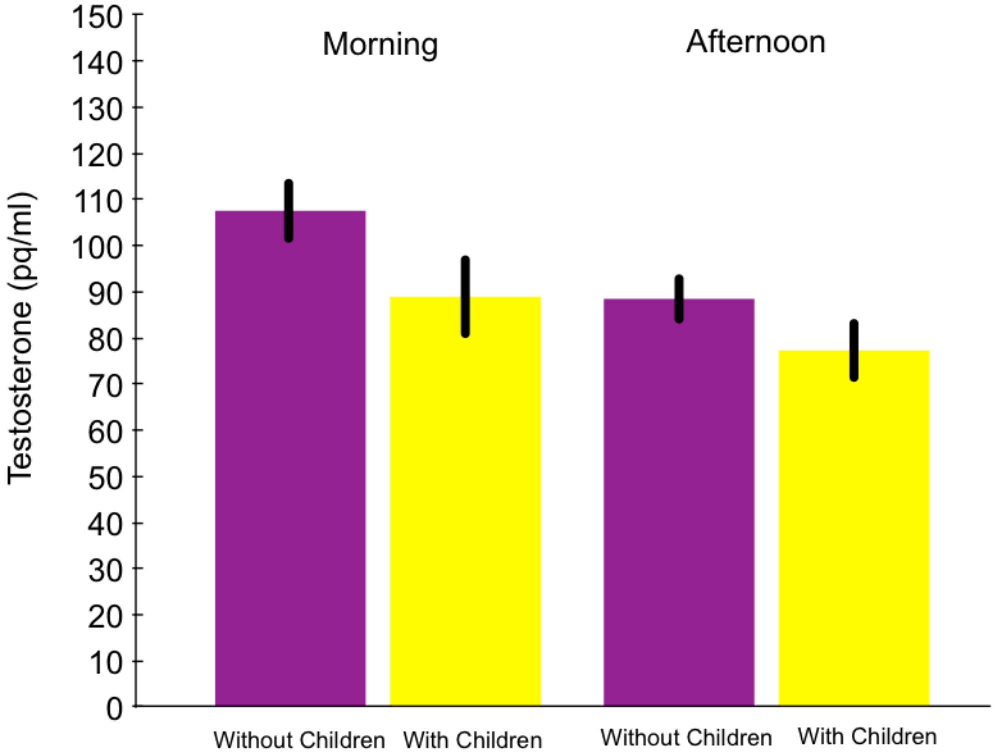

Figure 4: Estimated Marginal Means for Average Morning and Afternoon Testosterone by Co-Sleeping Status Among Married Men

Married men who reported sleeping in the same room as their children had significantly lower morning and afternoon testosterone than men who reported sleeping in different rooms to their children, independently of age, BMI, wage income, current financial status and village of residence (Table 4). The graph plots estimated marginal means, assuming mean values for age and BMI, no wage income, struggling or just about OK current financial status and residence in Keneba village. Error bars represent ±SE. Men who slept without children, n = 52; Men who slept with children, n = 25.