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Variation in testosterone levels and male reproductive effort: Insight from a polygynous human population

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ABSTRACT

Recent evidence suggests that, in humans, variations in testosterone (T) levels between men reflect their differential allocation in mating versus parenting efforts. However, most studies have been conducted in urbanized, monogamous populations, making generalizations from them questionable. This study addresses the question of whether indicators of male reproductive effort are associated with variations in salivary T levels in a polygynous population of agriculturists in rural Senegal. We first show that pair-bonding and/or transition to fatherhood is associated with T profiles: married fathers ($N=53$) have lower morning and afternoon T levels than unmarried non-fathers ($N=28$). Second, among fathers, individual differences in parenting effort, as well as variations in mating effort, predict morning T levels. Indeed, men highly investing in parental care show lower morning T levels. Moreover, among men under 50, polygynous men show higher morning T levels than monogamous men. Taken together with previous results in monogamous settings, these findings suggest that the endocrine regulation of reproductive effort is probably a general feature of human populations.

Introduction

Males in species that practice bi-parental care face a trade-off between acquiring mates and caring for offspring since mating effort and parental effort may overlap in time (Magrath and Komdeur, 2003). This trade-off, varying both between individuals (e.g. according to their mate value) and within individuals (e.g. according to their fatherhood status), is generally mediated by variations in androgen levels in various vertebrate species (Wingfeld et al., 1990). In birds for instance, natural variation in testosterone (T) underlies individual variation in the trade-off between mating and parenting efforts (McGlothlin et al., 2007) and experimentally produced elevation in T within individuals causes increases in mating effort and decreases in parental effort (reviewed in McGlothlin et al., 2007 and Muller et al., 2009). There is thus good evidence, at least in birds, that male reproductive strategy (i.e. relative investment in mating versus parental effort) is regulated through variation in T levels.

In humans, males also face a fundamental trade-off between mating and parenting efforts, since the human family is characterized by both relatively high levels of paternal investment and an extended period of child development highly dependent on adult care-giving (Geary, 2000). Nevertheless, the hormonal correlates of men reproductive strategy received little attention until the 1990s (see Booth and Dabbs, 1993 for a first study). There is now some evidence that T levels change at pair-bonding and/or transition to fatherhood in western monogamous societies. For instance, in the US, men in relationships (either married or not) have lower testosterone levels than single men (Burnham et al., 2003; Gray et al., 2002, 2004; van Anders and Watson, 2007). Furthermore, longitudinal studies among Canadian men have established that transition to fatherhood is associated with a decrease in T levels (Berg and Wynne-Edwards, 2001; Storey et al., 2000). The authors argue that lower T levels may facilitate paternal care in humans by decreasing the likelihood that a father will engage in competitive and/or mating behavior. To date, there are two studies outside North America, showing that fathers have lower T levels than non-fathers: in urban China (Gray et al., 2006) and in urban Jamaica (Gray et al., 2007b). These results suggest that lower testosterone levels are a common marker of fatherhood.

There is also some evidence that T levels reflect inter-individual variability in reproductive strategy. In Western countries, men producing more testosterone have more sexual partners (van Anders et al., 2007; van Anders and Watson, 2007) and are less likely to marry (Booth and Dabbs, 1993). Once married, high T men engage more often in extra-pair mating, experience higher marital conflict, and are more likely to divorce (Booth and Dabbs, 1993; Mazur and Booth, 1998). T levels are inversely related to the degree of investment men provide to their spouses (i.e., indirect paternal investment; Gray,

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Kahlenberg, Barrett, Lipson, and Ellison), and lower T men express more sympathy feelings in response to infant cries whether they are fathers or not (Fleming et al., 2002). The authors conclude that among human males, androgen levels are associated with nurturing tendencies and are predictive of paternal responsiveness.

The hormonal basis of male reproductive strategy is less documented in non-monogamous populations. However, humans are likely to have evolved in polygynous social systems (i.e. where men are allowed to marry several women), and polygyny is still the most prevalent mating system across human societies (more than 80% of the 139 societies recorded in the standard cross-cultural sample (Murdock and White 1980); Marlowe, 2000), which renders the study of polygynous populations particularly relevant to investigate the hormonal correlates of paternal care. As compared to monogamy, polygyny is characterized by a higher level of competition for access to mates (Draper and Harpending, 1988), which can possibly lead to differences in the hormonal correlates of parenting. However, mixed results have been obtained in polygynous populations in studies of hormonal correlates of either (1) pair-bonding/transition to fatherhood or (2) inter-individual variability in reproductive strategy.

First, the establishment of a pair-bond does not seem to be always followed by a decline in T levels. A study in Kenya revealed a difference between two polygynous societies: among Ariaal men (pastoralists), paired men have lower morning levels than unpaired men (Gray, Ellison, and Campbell, 2007a), which support the results obtained in industrialized societies, whereas in another study on Swahili men (practicing a mixed economy relying on farming, fishing, and tourism), unpaired men were similar to monogamously paired men (Gray, 2003). This unexpected result is partly attributed to specific events experienced by the unpaired Swahili men of their study sample ($N=17$), who either have previously been married ($N=11$) or have previously fathered children ($N=8$). These various results may also be attributed to variation across socio-ecologies in the reproductive strategy of men, the hormonal regulation of paternal care perhaps being more likely in populations expressing significant levels of paternal care. Using the standard cross-cultural sample, Marlowe (2000) showed that the level of paternal care (as measured by father–infant proximity) was a function of the subsistence mode, with highest levels of paternal care being expressed by foragers and lowest levels by pastoralists, agriculturalists being intermediate. The role of the subsistence mode in the relationship between male T levels and parental care was investigated more closely in a recent study of two populations in Tanzania: the Hadza (foragers) and the Datoga (pastoralists). As predicted, the relationship between men's involvement in offspring care and their testosterone levels was observed in foragers, but not in pastoralists (Muller et al., 2009). While the above results are promising, studies in non-Western societies are still rare, and some subsistence modes have not been investigated yet (e.g. agriculturalists). Therefore, more cross-cultural data are needed to assess the generality of the hormonal regulation of paternal care in humans.

Second, the inter-individual variability in reproductive strategy does not seem to be always associated with variations in T levels. As compared to monogamously married men (who are supposed to be mainly involved in parental efforts), polygynously married men (who are supposed to be mainly involved in mating efforts) were found to have either higher (among the Kenyan Swahili (Gray, 2003)) or similar T levels (among the Ariaal (Gray et al., 2007a)). The authors argue that this discrepancy may be due to several factors, and question the validity of using marital status as a proxy for mating effort. Indeed, in the populations studied so far, polygynous status is associated with important confounding variables regarding T levels: polygynously married men are older and have more children. As a result, the hormonal basis associated with variations between individuals in mating/parenting efforts is still poorly understood in polygynous populations, and additional proxies of male reproductive strategy are needed to properly investigate this question.

This study was designed to investigate the hormonal variations associated with male parenting and mating efforts in a polygynous population of agriculturalists, where a high level of paternal care is crucial to access limited resources such as food, education, and medical care. First, we studied variations in T levels in relation to the transition to fatherhood by comparing fathers and non-fathers. According to Marlowe (2000), agriculturalists are expected to show intermediate level of direct paternal care as compared to foragers and pastoralists. Given the positive correlation between paternal care and child condition in this population (Alvergne et al., 2009), we predict that fathers will show lower levels than non-fathers. Then, among fathers, we investigated variations in T levels in relation to male reproductive effort, using indicators of both mating effort and parental care. We predict that men highly invested in parental care and/or monogamously married men will have less T than men lowly invested in parental care and/or polygynously married.

Materials and methods

Both the Senegalese national committee of research council for health (CNRS) and the French national committee of informatics and liberties (CNIL) approved the protocols used to recruit participants and to collect data. Informed consent was obtained from all subjects.

Study population

The study was conducted in rural villages located in the Sine Saloum area of Senegal, West Africa. Villages are distributed around a city of c.a. 12,000 inhabitants and each village approximately counts around 300 individuals. In this area, the subsistence mode is mainly agriculture, especially cash crops like peanuts and cashew nuts, but also subsistence crops like millet. Economical resources are critical for access to education and health, which is very limited in Senegal, particularly in rural areas. In this country, the rate of maternal mortality during the 1998–2005 period is 401 deaths per 100,000 live births (for a comparison, the rate is 10 deaths per 100,000 live births in France). Because of limited access to medical care, the rate of mortality in children under 5 years is considerably higher than in occidental settings (116 deaths per 1000 in Senegal, and 5 per 1000 in France; http://www.unicef.org/). In such a situation, paternal investment is pivotal for physical (nutrition, health) and social well-being of the family. It represents however large costs for fathers in terms of time and energy spent in working activities.

In the studied population, the social system is patrilocal, and the inheritance mode patrilinear. Polygynous marriages are common, with a maximum of four wives, a threshold established by the Islamic religion, to which most people belong. Access to polygyny largely depends on age, and according to a larger sample of this population (110 families), 48% of men above 40 are polygynous while only 26% of men under 40 are. In this sample, polygynous men have on average more children than others (8.5 ± 3.9 for polygynous men and 5.2 ± 2.4 for monogamous men). Women's fertility in our study population is of 5.0 ± 2.5 children, which is consistent with the national fertility rate (5.3). For further information on the Senegalese population see Ndiaye and Ayad (2006).

Demographic data

A total of 81 men, aged 18–70 years were recruited from 4 villages. Selection of both the villages and the men was random, so this sample is likely to be representative of the larger community. Among them, 28 were non-fathers and unmarried, 32 were fathers and monogamously married, and 21 were fathers and polygynously married, with 2 ($N=13$), 3 ($N=7$) or 4 ($N=1$) wives. To homogenize the structure of the variable describing marital status, all polygynously married men were pooled in a single category. Anthropometric measurements (height, weight) were taken at the time of interviews. For each man, information was collected on age, number of children, socio-economic status and age of the youngest child in the family were collected. Age was estimated using ID cards. However, because age on ID cards is not always based on the birth certificate but is sometimes based on an administrative judgment, age was also assessed in relation to known ages of other men. To create a quantitative variable describing men's socio-economic status (SES), cattle and land possessions were recorded, and weighted by their average cost, estimated through independent reports of ten different men. For each child, information on his/her age, sex and birth order was collected (Table 1).

Assessment of individual differences in parenting/mating effort

A man's overall involvement in his family (including efforts to both maintain pair-bonding and take care for children) was assessed. For this purpose, mothers were asked to report their husbands' “overall” investment including both direct care of children and economic support for the family as: “very low”, “quite low”, “quite high”, or “very high”. Since sample repartition was unbalanced, the two lower levels were grouped into the label “low investing men” while the two higher levels were grouped into the label “high investing men”. To assess the global male mating effort in gaining access to mates, mothers were asked to report the number of nights per week their husband spent with them, and the level of jealousy-related conflicts they experienced: not at all (1), a little bit (2), a lot (3), very much (4). Before the survey, the questionnaire was translated into the local languages and recorded on a dictaphone. This procedure was used to conduct a private conversation between the mother and the researcher, thereby avoiding social biases associated with the presence of the locally known guide.

Quantification of T levels

T levels were measured in saliva samples. This non-invasive technique has been previously validated and yields T levels that are highly correlated with serum levels (Ellison, 1988; Read, 1993).

Saliva collection

Salicaps kits (IBL-Hamburg) were used to collect saliva. Each man was given labeled tubes and straws, and saliva was sampled on two consecutive days, twice a day: morning (9–11 AM) and afternoon (3–5 PM). Morning levels are usually considered to reflect the magnitude of the sleep-related rise in T, thus indicative of endogenous physiological differences between subjects while afternoon levels may be more indicative of behavioral and short-term ecological effects (Gray et al., 2007a). Participants were asked to rinse their mouth with fresh water and to wait 5 min before providing saliva. This procedure was controlled by A.A. or C.F., assisting the collection of each sample for each man. Samples were kept in a cool bag with blue ice blocks during a few hours before storage at −20 °C.

Table 1

Demographic and hormonal data according to marital status.

	Unmarried (mean ± SD)	Monogamous (mean ± SD)	Polygynous (mean ± SD)
Sample size	28	32	21
Age (years)	24.3 ± 7	42.1 ± 10.2	51.3 ± 10.3
Number of children	0.0 ± 0.0	5.5 ± 2.8	9.5 ± 4.2
SES (possessions in CFA × 10^3)	1928 ± 1,345	2555 ± 2,240	3116 ± 2,305
Morning T levels (pg/ml)	128.1 ± 44.5	67.5 ± 19.6	81.2 ± 41.0
Afternoon T levels (pg/ml)	94.2 ± 43.7	58.98 ± 21.3	70.9 ± 41. 3
Daytime T change (%)	−26.0 ± 24.2	−8.0 ± 32.8	−1.6 ± 44.8
Body mass index (BMI)	20.7 ± 1.9	22.3 ± 3.3	22.0 ± 2.8

Mean and standard deviation are indicated.

1 U of CFA corresponds to c.a. 0.0015 Euros and 0.002 US Dollars. Unmarried men are all non-fathers while married men are all fathers.

T assays

T levels in saliva were determined by Luminescence Immuno Assay (LIA) technique (Westermann, 2004), using LIA Testosterone kits (IBL, Hamburg). Saliva tubes were defrosted and centrifuged at 2,400 rpm for 10 min; 50 µl of standards, controls and samples were pipetted into wells of a microtiter plate; 50 µl of freshly prepared enzyme conjugate was added into each well, followed by 50 µl of testosterone antiserum. The plate was allowed to stand for 4 h at room temperature, then the content of all wells was discarded, and the plate was washed 4 times using 250 µl of diluted wash buffer. 50 µl of the chemiluminescence reagent was introduced into each well and allowed to stand 10 min before relative luminescence units (RLU) were measured with a luminometer. A total of seven standards (0 to 760 pg/ml) were used to calibrate the assay curve. The obtained RLU of the standards were plotted against their concentrations, allowing the calculation of sample concentration directly from the standard curve (using Microwin software). The sensitivity of this technique is 2.5 pg/ml at 30–110 pg/ml. The four saliva samples of each participant were run in duplicate and had a mean intra-assay CV of 5.5%. Inter-assay CV for testosterone measurements were 10.1% for low controls and 8.0% for high controls.

Statistical analysis

Correlations between variables were calculated using the non-parametric Spearman's rank correlation test. To investigate the effects of several independent variables on T levels, linear models were used. Three dependent variables were investigated: morning T levels (average of the two morning samples), afternoon T levels (average of the two afternoon samples) and percentage daytime T change (to investigate daytime T change during the day, average afternoon T levels was entered as the dependent variable and morning T level was entered as a confounding variable in each model). Box Cox transformations were performed to normalize dependent variables when needed. For each analysis, a full model was built and was not submitted to stepwise simplification. This procedure was used to decrease the number of false positives, and thus to provide conservative results (Whittingham et al., 2006). A first analysis was conducted to investigate the effects of age, body mass index (BMI) and socio-economic status (SES); these were suggested to be putative confounding factors for T levels in subsistence populations (Ellison et al., 2002; Lukas et al., 2004). Only the variables that were significant in this first analysis were included as independent variables in other models, in order to increase sample size (due to the presence of some missing values for BMI and SES). The significance of the terms was evaluated by *F*-tests and the normality of residuals was tested for each model. All statistical analyses were carried out using R software (R 2.4.1, 2006).

Results

Testosterone (T) variations

T levels ranged from 22.4 to 223.2 pg/ml (mean ± SD: 93.6 ± 44.6) in the morning and from 21.1 to 187.9 pg/ml (mean ± SD: 74.8 ± 38.3) in the afternoon. Average T levels (average of morning and afternoon levels) were correlated between the two sampling days (Spearman's correlation test, $\rho = 0.51$, $P < 0.001$). Additionally, morning T levels (average of morning T levels) were correlated with average afternoon T levels (Spearman's correlation test, $\rho = 0.58$, $P < 0.001$). During the day, T levels always declined in unmarried non-fathers on average

(-26.0 ± 24.2 pg/ml), while it is not the case for married fathers (monogamous men: -8.0 ± 32.8 pg/ml; polygynous men: -1.6 ± 44.8 pg/ml). Men in the present study had lower T levels than has been recorded for men from western societies using similar saliva assays (Goncharov et al., 2006). This is consistent with reported T levels from other non-western populations (Bribiescas, 2001; Ellison, 2003).

Influence of age, body mass index (BMI) and socio-economic status (SES)

Morning T levels were negatively associated with age ($F_{1,49} = 16.90$, $P<0.001$) but independent from both BMI ($F_{1,49} = 0.31$, $P = 0.58$) and SES ($F_{1,49} = 1.39$, $P = 0.24$). The model was significant ($F_{3,49} = 8.65$, $P<0.001$) and normality of residuals was not rejected (Shapiro test, $W = 0.97$, $P = 0.50$). Afternoon T levels were negatively associated with age ($F_{1,49} = 3.57$, $P = 0.06$) but independent of both BMI ($F_{1,47} = 0.02$, $P = 0.87$) and SES ($F_{1,49} = 0.80$, $P = 0.37$).

The percentage of change in T during the day (100 × (average afternoon levels − average morning levels)/average morning levels) was found to be positively related to age ($F_{1,49} = 5.6$, $P = 0.02$), but independent from both BMI ($F_{1,49} = 0.55$, $P = 0.5$), and SES ($F_{1,49} = 0.00$, $P = 1.0$).

Testosterone and fatherhood status

Morning T levels, afternoon T levels and daytime T change (afternoon levels controlled for morning levels) were compared between fathers and non-fathers. First, fathers had lower morning T than non-fathers ($F_{1,62} = 5.71$, $P = 0.02$). This effect was controlled for age ($F_{1,62} = 7.46$, $P< 0.01$) and for the interaction between age and fatherhood status ($F_{1,62} = 2.99$, $P = 0.09$). Similarly, fathers had lower afternoon T than non-fathers ($F_{1,63} = 4.74$, $P = 0.03$). This effect was controlled for age ($F_{1,63} = 0.00$, $P = 0.93$) and for the interaction between age and fatherhood status ($F_{1,62} = 2.99$, $P = 0.09$).

In contrast, daytime change in T levels did not differ between fathers and non-fathers. Indeed, afternoon T levels did not differ between fathers and non-fathers ($F_{1,61} = 0.66$, $P = 0.41$) when controlling for morning T levels ($F_{1,61} = 26.94$, $P< 0.001$) and there was no significant interaction between age and fatherhood status ($F_{1,61} = 0.48$, $P = 0.48$).

Hence, morning and afternoon T levels, but not daytime T change, depend on fatherhood status (Fig. 1).

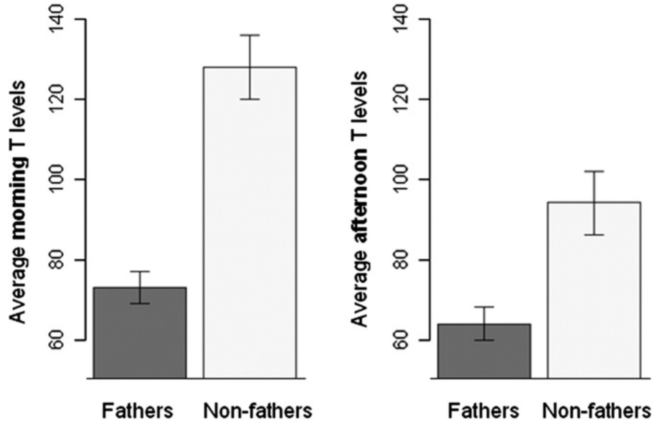

Fig. 1. Mean ± s.e.m. of average morning and afternoon T levels (pg/ml) as a function of fatherhood status (Raw data: $N_{\text{Fathers}} = 56$; $N_{\text{Non-fathers}} = 31$). In the multivariate analyses controlled for the interaction between men's age and fatherhood status, fathers have significantly lower T levels than non-fathers at both time of the day (morning: $F_{1,62} = 5.71$, $P = 0.02$; afternoon: $F_{1,63} = 4.74$, $P = 0.03$). See text for details.

Testosterone, mating and parenting efforts

Among fathers, the relationships between variables describing parental and mating efforts and morning T levels, afternoon T levels and daytime T change were investigated.

Morning T levels. The number of children was highly correlated with father's age (Spearman correlation, $\rho = 0.75$, $P< 0.001$), precluding inclusion of both variables in the same model. Two models were built, differing only by one fixed effect (either the number of children or age), but only the one that contained age was retained, as this was the one which explained the most variance in morning T levels. This is consistent with the fact that the father's age is the variable that is the most correlated with the response variable. Indeed, morning T levels were previously found to largely depend on age (see previous section), and were not correlated with the number of children (Spearman's correlation, $\rho = 0.11$, $P = 0.5$). Additionally, as morning T levels decline with age in polygynous men (Spearman's correlation, $\rho = -0.53$, $P = 0.02$) but not in monogamous men (Spearman's correlation, $\rho = -0.02$, $P = 0.9$), the significant effect of the interaction between age and marital status was included ($F_{1,30} = 4.28$, $P< 0.05$). Before age 50, polygynous men have higher morning T levels than monogamous men, where this tendency is reversed when men are older than 50 years old (Fig. 2). Morning T levels did not depend on age of the father's youngest child ($F_{1,30} = 0.04$, $P = 0.8$), the number of nights slept with the mother per week ($F_{1,30} = 0.98$, $P = 0.3$) or jealousy conflicts between them ($F_{1,30} = 1.05$, $P = 0.3$). Morning T levels were negatively associated with levels of paternal investment as reported by the mothers ($F_{1,30} = 5.81$, $P = 0.02$). Thus, fathers considered by their wives as less concerned by parental care were those who had the higher morning T levels and this relationship is found for both polygynous and monogamous men (Fig. 3). Overall, when men are under 50, polygyny and low investment status are associated with high morning T levels, whereas monogamy and high degrees of investment are associated with low morning T levels.

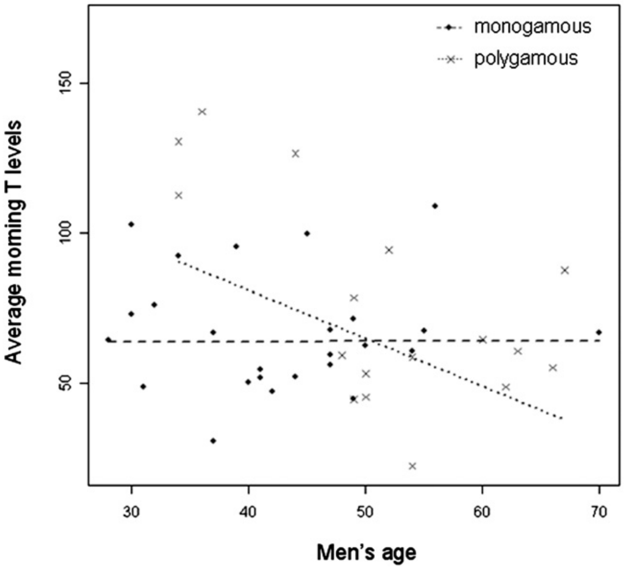

Fig. 2. Variation of morning T levels (pg/ml) among fathers as a function of age and marital status. Raw data are indicated by dots. Lines indicate the predicted relationships between morning T levels and age for either monogamous or polygynous men. A negative relationship is observed for polygynous fathers but not for monogamous ones ($F_{1,30} = 4.28$, $P< 0.05$; see text for details). For men younger than 50 years old, polygynous fathers have higher morning T levels than monogamous fathers, while it is the reverse for older men.

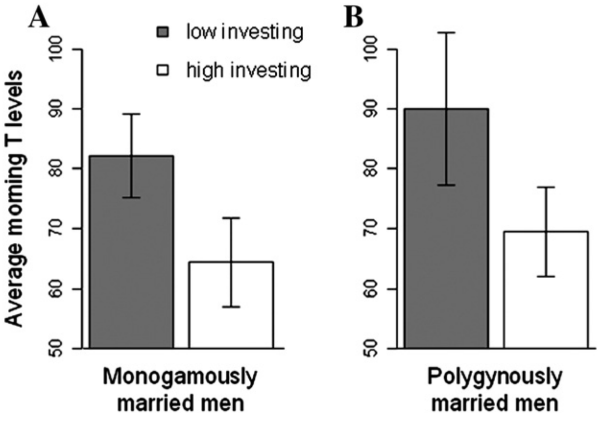

Fig. 3. Morning T levels (pg/ml) as a function of a man's involvement in his family (Raw data). (A) monogamously married men ($N_{\text{Low investing}} = 7$; $N_{\text{High investing}} = 23$). (B) Polygynously married men ($N_{\text{Low investing}} = 5$; $N_{\text{High investing}} = 14$). In the multivariate analyses controlling for the interaction between men's age and marital status, low investing men have significantly lower T levels than high investing men ($F_{1,30} = 5.81$, $P = 0.02$). See text for details.

Afternoon T levels. To determine whether father's age or number of children should be included in the analysis, we used the same method as described for morning T levels. The model containing father's age was retained, as it explained the largest proportion of the variance. In this model, afternoon T levels did not depend on either father's age ($F_{1,32} = 0.13$, $P = 0.72$), age of the father's youngest child ($F_{1,32} = 1.10$, $P = 0.30$), number of nights slept with the mother per week ($F_{1,32} = 0.10$, $P = 0.75$) or jealousy conflicts reported by mothers ($F_{1,32} = 0.17$, $P = 0.68$). Moreover, it was not related to either marital status ($F_{1,32} = 0.00$, $P = 0.99$) or levels of paternal investment as reported by the mothers ($F_{1,32} = 1.07$, $P = 0.30$). Thus, in this sample, afternoon T levels were not significantly related to reproductive strategy.

Daytime T change. The percentage of change in T during the day is marginally associated with age (Spearman's correlation, $\rho = 0.28$, $P = 0.07$), but not with the number of children (Spearman's correlation, $\rho = 0.07$, $P = 0.6$). Because of their strong association (see above), both variables were not entered in the same model, so two models were built, differing only by one fixed effect (either the number of children or the age). The model explaining the most variance was retained, containing the father's age, which is the variable that is the most correlated with the response variable. Variations in afternoon T levels, when controlled for morning levels ($F_{1,29} = 5.16$, $P = 0.03$) are not predicted by father's age ($F_{1,29} = 0.56$, $P = 0.46$), marital status ($F_{1,29} = 0.09$, $P = 0.76$), or the interaction between these two variables ($F_{1,29} = 1.04$, $P = 0.31$), levels of paternal investment ($F_{1,29} = 0.10$, $P = 0.74$), age of the youngest child ($F_{1,29} = 0.86$, $P = 0.36$), number of nights slept with the mother per week ($F_{1,29} = 0.25$, $P = 0.8$), or jealous conflicts ($F_{1,29} = 0.56$, $P = 0.45$). The model was not significant ($F_{8,29} = 1.24$, $P = 0.3$). Contrary to morning T levels, variations in T levels during the day cannot be predicted by either mating or parenting effort.

Discussion

This study investigated the relationship between mens' salivary T and the trade-off between mating and parenting efforts in a polygynous population of agriculturists from rural Senegal. The men's reproductive trade-offs were evaluated by recording (1) their pair-bonding/fatherhood status and (2) their behavioral profile in the allocation of parental care and their marital status (i.e. monogamously married; polygynously married). Our findings generally fit the theoretical framework that predicts an association between elevated male T and mating efforts (e.g., mate seeking) on one hand, and between lowered T levels, pair-bonding, and paternal care on the other hand (Gray et al., 2002).

T levels, the establishment of a pair-bond and/or the transition to fatherhood

After controlling for age, we found that married fathers have significantly lower morning and afternoon T than unmarried non-fathers. This is consistent with results obtained in some east-African populations, where both morning and afternoon levels are predicted by marital status (in the Ariaal, Gray et al., 2007a), or presence of children in the household (in the Hadza, (Muller et al., 2009)). Given the structure of the data, the effects of fatherhood and marriage cannot be disentangled. However, this structure reflects the local social system, where fatherhood generally occurs just after marriage, and this has most likely been the rule across human evolutionary history. The association between lower T levels and either fatherhood or bonding was previously reported in monogamous populations (Gray et al., 2004, 2007b, 2006), suggesting that a decrease in T levels is a general marker of parenting. Interestingly, several studies have reported that the transition to fatherhood is associated with a decrease in androgen levels in various other bi-parental species, including some fish (Knapp et al., 1999), birds (McGlothlin et al., 2007), mammals (review in Wynne-Edwards and Reburn, 2000) and primates (Maestripieri, 1999; Nunes et al., 2000; Ziegler, 1996). Moreover, this pattern seems to be absent in species where mothers are the only caretakers (Reburn and Wynne-Edwards, 1999), which further supports the role of the endocrine system in the mediation of paternal behavior in animals.

T levels, parental and mating efforts

First, our study showed that a man's overall involvement in his family, as reported by the mothers, varies with morning (but not afternoon) T levels in men, controlling for age, marital status (i.e. monogamously or polygynously married) and their interaction. The finding that low T levels are associated with a high investment in parenting is in agreement with previous studies in urban, monogamous populations where, among married men, low T levels are a predictor of a high degree of investment in spouses (i.e., indirect parental effort) (Gray et al., 2002), and high T levels are associated with a high probability of divorce, extra-marital sex and marital conflict (Booth and Dabbs, 1993; Mazur and Booth, 1998). However, previous studies on behavioral variations usually reported a stronger correlation with afternoon as compared to morning levels (reviewed in Muller et al., 2009). This tendency was attributed to the fact that afternoon T levels are influenced by the cumulative outcomes of diurnal social interactions, while morning levels are not. Data on the nature and frequency of social interactions in men on the sampling days were however not recorded, thus precluding controlling for potential confounding differences between groups. Morning levels are nevertheless thought to reflect endogenous physiology (Gray, 2007a), which could be interpreted as an indicator of male behavioral profile. Further investigations on the relative importance of morning versus afternoon levels to explain male reproductive strategy are warranted.

Second, we showed that morning T levels were higher among polygynously married men than among men that were monogamously married, but only if men were younger than 50. This could be interpreted as a correlate of the male mating behavior, but it may also reflect an increase in mate guarding with the number of wives, and additional data on the level of physiological stress (i.e. cortisol) could help to tease apart these two possibilities. When men get older than 50, a reversed pattern is observed, with polygynously married men having lower T levels than monogamously married men. This intriguing result has also been reported for Ariaal men older than 40 (Gray et al., 2007a), and suggests that the ability to attract mates at older ages is not a correlate of higher T levels but rather an effect of age on wealth. Indeed, in the present population, the ability to obtain wives increases with socio-economic status (Kendall rank correlation, $N = 45$, $P = 0.001$), which in turn increases with age (Kendall rank correlation, $N = 45$, $P = 0.01$).

Nevertheless, why T levels are lower in polygynously married men than in monogamously married men remain intriguing, although we must acknowledge that the sample size of men older than 50 is relatively small ($N_{\text{polygynous}} = 8$; $N_{\text{monogamous}} = 6$). One explanation for this effect (if it is not due to a sample bias) could be that the difference between polygynously and monogamously married men in their number of children, and thus in their investment in paternal related activities, is more evident at older age, leading T levels to decrease more steeply in polygynously married men. However, the number of children is not correlated with T levels in this population (Kendall rank correlation, $N = 42$, $P = 0.65$). Another possible explanation is that polygyny accelerates senescence in men due to high and long-term efforts in both mate guarding and family provisioning as compared to other men. Longitudinal studies would here be needed to determine whether or not this is actually the case in this population. To conclude, the ability to marry polygynously is possibly driven by different forces depending on the age considered, and effects of male reproductive strategy are more likely to be expressed at younger ages.

Age, T levels and body mass index

We found that T levels decrease as a function of age. Although this link is not universal, it has been observed in USA, Congo and Zimbabwe, but not in Nepal, Paraguay and Ariaal men in Kenya (Ellison et al., 2002, Lukas et al., 2004; Gray et al., 1991, 2007a; Vermeulen and Kaufman, 1995). It is worthy of note that inter-population differences in T levels were found to be more pronounced for young men (15–30 years) than for older men (45–60 years) (Ellison, 2003). The authors conclude that the differences between populations in patterns of T decline with age result from variations in peak levels during young adulthood and are thus highly dependent on the reproductive physiology of young males. Indeed, under the 'challenge' hypothesis, testosterone increases the males' readiness to compete during the life history stages where reproductive opportunities are the greatest (Archer, 2006; Wingfeld et al., 1990). In the present case, Senegalese young men are likely to experience a high degree of competition for access to mates, because of the possibility of polygynous marriages, and interestingly the effect of age is found for polygynous men but not for monogamous men. Why Ariaal men, also polygynous, do not show a similar age pattern is intriguing. It could be that the availability of mates is different between the two populations, generating different levels of competition among young men, and thus different age patterns.

One would have expected the decline of T with age in our population to be associated with a decline in body mass index. Indeed, age is assumed to influence the role of T in maintaining somatic function (Bribiescas, 2001). However, in the present population, BMI does not predict variations in T levels. The role of nutritional condition for T levels in adult males is not generally agreed upon, and results largely depend on the index chosen. There is some evidence that BMI decreases with age in the Ariaal of Kenya (Campbell et al., 2003) and in Zimbabwe (Lukas et al., 2004), although it does not in the Lese of Zaire (Bentley et al., 1993), or the Tamang and Kami of central Nepal (Ellison and Panter-Brick, 1996), or among Turkana males of Kenya (Campbell et al., 2005). The collection of other indexes such as the fat free mass index, taking into account muscle mass, would help to confirm the absence of a link between T levels and body mass index in this population.

In summary, our study showed that T levels in a polygynous population are associated with both men's behavioral profiles for paternal care and their life stage concerning the establishment of pair-bond and/or the transition to fatherhood, suggesting that both inter-individual variations and lifetime regulations of T levels modulate men's parenting efforts in this population. Taken together and with previous studies on monogamous populations, our findings indicate that the regulation of male reproductive trade-offs through the endocrine system is a common feature of human populations. Nevertheless, as human paternal care exhibits cultural variations (Geary, 2000; Marlowe, 2000), additional studies in societies exhibiting very high or very low paternal care are warranted to confirm the generality of hormonal correlates of male reproductive strategies.

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