Testosterone and paternal care in East African Foragers and Pastoralists

1

2

Testosterone and paternal care in East African foragers and pastoralists

4

5

6

Martin N. Muller[1,4,]*, Frank W. Marlowe[2,4], Revocatus Bugumba[3]

& Peter T. Ellison[4]

9

10

11

12

[1]Department of Anthropology, University of New Mexico, Albuquerque, New Mexico

87131, USA

[2]Department of Anthropology, Florida State University, Tallahassee, Florida 32306, USA

[3]Archaeology Unit, University of Dar es Salaam, Dar es Salaam, Tanzania

[4]Department of Anthropology, Harvard University, Cambridge, Massachusetts 02138,

USA

19

20

To whom correspondence should be addressed. E-mail: muller@unm.edu

22

23

24

1 **Summary**

2 The "challenge hypothesis" posits that testosterone facilitates reproductive effort

3 (investment in male-male competition and mate-seeking) at the expense of parenting

4 effort (investment in offspring and mates). Multiple studies, primarily in North America,

5 have shown that men in committed relationships, fathers, or both maintain lower levels of

6 testosterone than unpaired men. Data from non-western populations, however, show

7 inconsistent results. We hypothesized that much of this cross-cultural variation can be

8 attributed to differential investment in mating vs. parenting effort, even among married

9 fathers. Here we directly test this idea by comparing two neighboring Tanzanian groups

10 that exhibit divergent styles of paternal involvement: Hadza foragers and Datoga

11 pastoralists. We predicted that high levels of paternal care by Hadza fathers would be

12 associated with decreased testosterone in comparison to non-fathers, and that no such

13 difference between fathers and non-fathers would be evident in Datoga men, who provide

14 minimal direct paternal care. Twenty-seven Hadza men and 80 Datoga men between the

15 ages of 17 and 60 provided morning and afternoon saliva samples from which

16 testosterone was assayed. Measurements in both populations confirmed these predictions,

17 adding further support to the hypothesis that paternal care is associated with decreased

18 testosterone production in men.

19

20 **Key Words**

21 Fatherhood, parenting effort, challenge hypothesis, mating effort, Hadza, Datoga

22

23

1   **Introduction**

2   Humans are unique among primates in forming long-term pair bonds in the

3   context of multi-male, multi-female social groups, despite men and women typically

4   spending most of their waking hours in separate locations (Rodseth et al. 1991). Humans

5   are also exceptional among mammals for their level of direct parental investment, which

6   in foraging societies can extend for almost two decades (Kaplan 1997, Kaplan et al.

7   2000). This rare combination of traits links female reproductive success to male

8   investment, while presenting both sexes with continual opportunities for extra-pair

9   copulation. Consequently, human males face a fundamental trade-off between allocating

10   resources toward mating effort (investment in male-male competition and mate

11   attraction) and parenting effort (investment in offspring and mates), with the optimal

12   pattern of allocation dependent on local social and ecological constraints (Trivers 1972,

13   Lancaster & Kaplan 1992, Marlowe 2003a).

14   The endocrine system plays an important role in modulating life-history

15   strategies, such as reproductive effort, by coordinating morphological, physiological and

16   behavioral responses to environmental factors, such as energy availability and social

17   context (Wingfield et al. 2000, Ellison 2003). In a range of vertebrates, the steroid

18   hormone testosterone has been shown to play a critical role in mediating the trade-off

19   between mating effort and parenting effort. The evidence for this effect is particularly

20   clear in birds, which show dramatic interspecific and individual differences in temporal

21   patterns of testosterone secretion, explicable by variation in two key variables: intensity

22   of male mating competition and degree of paternal care (Wingfield et al. 1990, Beletsky

23   et al. 1995, Wingfield et al. 2000). Data from more than 60 avian species are consistent

1　with the "Challenge Hypothesis" (Wingfield et al. 1990, Hirschenhauser & Oliveira

2　2006), which proposes that testosterone levels increase when males must respond to

3　threats from conspecifics - particularly during territory formation and mate guarding -

4　and decrease during periods when males must provide care to offspring (Wingfield et al.

5　2000). Experimental manipulations of male birds have confirmed that high levels of

6　testosterone suppress parental behavior in favor of male-male competition (Hegner &

7　Wingfield 1987, De Ridder et al. 2000, Peters et al. 2002). In a number of mammals that

8　exhibit paternal care, male testosterone levels also decrease from the period of gestation

9　to lactation (Roberts et al. 1996, Brown et al. 1995, Reburn & Wynne-Edwards 1999,

10　Nunes et al. 2000).

11　　　　Although numerous studies have investigated the role that testosterone plays in

12　facilitating aggression and status-seeking behavior in men (reviewed in Archer 2006),

13　until recently, few had addressed the hypothesis that pair-bonding and paternal care are

14　associated with low levels of testosterone. In the 1990's, two studies of military personnel

15　found that married men exhibited slightly lower testosterone levels than unmarried men,

16　though the difference was modest (Booth & Dabbs 1993, Mazur & Michalek 1998).

17　Subsequently, Storey et al. (2000) reported that in 34 couples taking childbirth classes,

18　men exhibited chronic declines in testosterone production over the course of the

19　pregnancy. They also exhibited acute decreases in circulating testosterone in response to

20　visual, tactile, olfactory, and auditory stimuli associated with paternal care (i.e. when

21　listening to a tape of a crying baby, and holding a doll that had been wrapped in a blanket

22　worn by a real baby). A related study by Berg and Wynne-Edwards (2001) showed that,

23　in comparison to control men, a sample of fathers in pre-natal classes had decreased

4

1 testosterone in the weeks surrounding parturition. More recently, a series of cross-

2 sectional studies have variously demonstrated that either men in committed, long-term

3 relationships, fathers, or both have lower levels of testosterone than unpaired men (Gray

4 et al. 2002, Burnham et al. 2003, Gray et al. 2004a, Gray et al. 2004b, McIntyre et al.

5 2006).

6   Most of the studies showing an effect of marriage and fatherhood on men's

7 testosterone have examined North American populations living under conditions of

8 relative energy abundance. Data from less affluent, non-western populations show

9 inconsistent results. One study in Beijing revealed significantly lower testosterone levels

10 in married fathers than in non-fathers, but no significant difference between married and

11 unmarried men without children (Gray et al. 2006). No significant difference was

12 apparent in testosterone levels between married and unmarried men in Dominica (Flinn et

13 al. 1998), nor among Kenyan men on the island of Lamu (Gray 2003). In the latter

14 population, polygynously married men actually exhibited higher levels of testosterone

15 than monogamously married men. Among Ariaal pastoralists in northern Kenya, the

16 transition from life as a bachelor and warrior to monogamous marriage was associated

17 with lower testosterone levels (Gray et al. 2007).

18   Cross-cultural variation in testosterone responses to marriage and fatherhood

19 could potentially result from differential patterns of investment in mating and parenting

20 effort, even among married fathers (Muller & Wrangham 2001). For example, McIntyre

21 et al. (2006) showed that within an American undergraduate population, pair-bonded men

22 who maintained a strong interest in sexual activity with women other than their primary

23 partner exhibited higher testosterone levels than those who favored fidelity. If North

1 American men typically invest more in marital bonds and paternal care than men in, for

2 example, polygynous societies, then this might account for the more predictable

3 association between reduced testosterone and fatherhood in these populations (Gray

4 2003, Gray et al. 2007).

5   The purpose of this study is to directly test the relationship between paternal care

6 and testosterone in men by comparing two neighboring Tanzanian groups that exhibit

7 divergent patterns of paternal involvement: Hadza foragers and Datoga pastoralists.

8 These populations provide an ideal test case because they live in close proximity around

9 Lake Eyasi in northern Tanzania, but their cultural norms of parenting reflect a broader

10 ethnographic pattern in which foragers often maintain close father-infant bonds, while

11 pastoralists tend to show lower levels of direct paternal care (Marlowe 2000; Figure 1).

12   Specifically, among the Hadza most marriages are monogamous (with

13 approximately 4% of men having two wives at any given time), and most couples

14 (approximately 68%) co-reside in a camp with the wife's mother (Woodburn 1968,

15 Marlowe 1999a, 2003b). Hadza men exhibit high rates of direct paternal care, including

16 carrying, holding, cleaning, feeding and pacifying infants, with biological children

17 receiving significantly more care than stepchildren (Marlowe 1999a, 1999b, 2005). In

18 focal follows, Marlowe (2005) observed Hadza men holding their infants 5.6% of the

19 time in daylight and evening hours. When fathers with children under 3 years of age were

20 present in camp, they spent more than 20% of their time interacting with those children

21 (2005). Fathers also slept in close proximity to offspring at a shared hearth, and were thus

22 in contact with children from approximately 21:00 to 07:00 (2005).

1   A very different pattern of paternal care is evident among the Eyasi Datoga,

2 patrilineal pastoralists with a strong "warrior tradition" (Klima 1970). Approximately

3 40% of Datoga families are polygynous, living in widely spaced individual homesteads

4 consisting of a thorn-bush fence in the shape of a figure-eight, half of which contains

5 living huts, and the other half a corral for herds of cattle, sheep and goats (Klima 1970,

6 Borgerhoff Mulder 1992, Sellen 1999). Datoga men spend much of their day away from

7 their homesteads, herding cattle, visiting other men, and traveling to markets (Klima

8 1970, Sellen 1999). When at their homesteads, men take their meals in a separate men's

9 hut, and sleep in a separate room from their wives and children (Klima 1970). Although

10 men sometimes interact with older children, particularly those who have started to help

11 tend herd animals, direct interaction with infants is minimal, and men express a strong

12 belief that caring for infants is "women's work" ("*kazi ya wanawake*" was the Kiswahili

13 phrase employed by multiple informants). Before weaning, mother and infant are

14 considered to be "one body," just as they were prior to parturition (Blystad & Rekdal

15 2003).

16   Accordingly, the challenge hypothesis makes two predictions about fathers'

17 testosterone levels in these populations. First, Hadza men caring for young children are

18 expected to maintain lower levels of testosterone than men not engaging in paternal care.

19 Second, Datoga men with young children in their homesteads should show no difference

20 in testosterone from men who do not have offspring.

21   A third hypothesis is suggested by Storey et al.'s (2000) data demonstrating an

22 acute suppressive effect of infant cues on paternal testosterone production. Because

23 Hadza men's direct paternal care (infant holding, feeding, and caregiving) peaks around 9

1   months after parturition, and decreases steadily thereafter as offspring mature (Marlowe

2   2005), Hadza fathers with relatively young children are exposed to infant stimuli at

3   elevated rates throughout the day. Consequently, such fathers are expected to exhibit a

4   more pronounced diurnal decline in testosterone than fathers of older children (e.g. Gray

5   et al. 2002). Accordingly, Hadza, but not Datoga, fathers are predicted to show a

6   correlation between age of the youngest child and the relative decrease in testosterone

7   levels from morning to evening.

8

9   **Methods**

10   In most western populations, free testosterone levels peak during young adulthood

11   and decline steadily thereafter with age (Vermeulen et al. 1999). By contrast, in many

12   non-western populations, men exhibit comparatively lower testosterone levels in early

13   adulthood, and thereafter show little or no reduction (Ellison et al. 2002). In this study we

14   restricted our sample to men between the ages of 17 and 60 in order to eliminate variation

15   in testosterone resulting solely from disparate maturation rates in younger men, or the

16   effects of ill health in older men, that might be mistaken for an age effect (e.g. Muller et

17   al. 2003).

18   Eighty Datoga participants between the ages of 18 and 59 were recruited by word

19   of mouth in and around the villages of Mangola and Matala, along Lake Eyasi, during

20   August 2003. Interviews were conducted either in Kiswahili, by R. Bugumba and M.

21   Muller, or in Kidatoga, with the assistance of an experienced Datoga field assistant.

22   Questions focused on men's ages, and their marital and reproductive histories. Thirty-two

23   men in the sample had no children and, of those, 25 had no wife. Of the 48 men who had

1   children, all were married (12 polygynously), with the age of the youngest child ranging

2   from less than one month to 11 years (mean=2.24 years). Most young men knew their

3   date of birth; for older men, this was estimated with reference to major political and

4   social events (e.g. Tanzanian Independence, 1961), and in relation to known ages of other

5   men. Anthropometric data included measures of height and weight, together with body

6   fat estimates from a bioelectrical impedance scale (Tanita BF522). BMI was calculated

7   as: weight(kg)/height^2(m).

8   Twenty-seven Hadza participants between the ages of 17 and 51 were recruited in

9   the Sipunga area, east of Lake Eyasi, during January 2004. Collection of saliva samples

10   was coordinated by R. Bugumba. F. Marlowe collected anthropometric data and

11   conducted interviews (in Kiswahili) with adult Hadza to gather data on marital status and

12   number, ages, and residential status of children. Fifteen of the Hadza participants either

13   had no children (n=6), or were not involved in caring for presumed children because they

14   had separated from the mother (n=9). None of the 15 was residing with a stepchild. These

15   men were classified as "non-fathers." Ten Hadza men had presumed biological children

16   (ages ranging from less than one month to 7 years; mean=3.2 years) that they were

17   actively nurturing, provisioning and sharing a hearth with ("fathers"). Two men had no

18   children, but were expecting with their pregnant spouses. These two men were excluded

19   from analyses comparing fathers and non-fathers. However, including them in the former

20   group as "expectant fathers" (as per Storey et al. 2000, Berg & Wynne-Edwards 2001)

21   had no effect on any of the father/non-father comparisons (see below). Hadza ages were

22   known with greater precision than those of the Datoga, because births have been recorded

1   for several decades as part of a long-term demographic study (Blurton Jones et al. 1992,

2   Marlowe in press).

3   In order to control for diurnal variation in testosterone levels (Van Cauter 1990),

4   we collected both morning and afternoon samples from each subject during specified

5   hours. For Datoga subjects, one morning sample was collected between 7:34 and 8:18,

6   and one evening sample between 17:45 and 19:03. Two Datoga men contributed matched

7   morning and evening samples on two separate days, and for these individuals the average

8   of each pair was used in all analyses. Nine Datoga men failed to return for evening

9   sample collection, so only their morning samples were available for analyses. Hadza

10   subjects contributed matched morning (7:10-8:35) and evening (17:00-18:00) samples on

11   1-3 different days (median=3), and median values for each man were used in all analyses.

12   All participants avoided eating, drinking, chewing or smoking for 30 minutes, and

13   rinsed their mouths with a small amount of clean water, prior to sample collection.

14   Trident sugarless gum was provided to stimulate saliva production, and sodium azide was

15   subsequently added to sample tubes to inhibit bacterial growth. Samples were maintained

16   at ambient temperature for 4-6 weeks before being transported to Harvard University,

17   where they were stored frozen at -20° C until April 2004, when they were assayed for

18   testosterone. Lipson and Ellison (1989) have previously validated all sample collection

19   and storage procedures. Informed consent was obtained from all participants, and the

20   Human Subjects Committee at Harvard University approved all research protocols.

21   Testosterone assays were performed by the first author in the Reproductive

22   Ecology Laboratory at Harvard University, using a modified application of the I^{125} double

23   antibody kit from Diagnostic Systems Laboratories (Webster, TX). Sample and standard

1 reactions were run in duplicate. Substrate (150 ml) was pipetted into borosilicate tubes

2 containing either 100 ml of sample and 50 ml of buffered saline or, for the standard

3 reactions, a 400 pg/ml standard concentration in volumes of 2.5, 12, 30, 75, and 150 ml,

4 with volumes of buffered saline adjusted to yield 150 ml total volume. Antiserum, diluted

5 1:3 (100 ml), and undiluted tracer (200 ml) were added to sample and standard tubes.

6 Reactions incubated overnight, after which precipitating reagent (400 ml) was added,

7 tubes were centrifuged, and aspirated. The assays were sensitive to 14 pmol/L T, and the

8 interassay coefficient of variation was 7.9%.

9 All comparisons between independent groups employed the Mann-Whitney U

10 test, and dependent groups the Wilcoxon signed ranks test. All correlations report

11 Spearman's rank correlation coefficient (ρ). All statistical tests are 2-tailed. Unless

12 otherwise indicated, means are reported ± SE.

13

14 **Results**

15 The two study populations were comparable in terms of age and anthropometry

16 (Table 1). Datoga men are generally taller than Hadza men, and this resulted in

17 significant differences between the groups in both height ($n_d=80$, $n_h=27$, Z=-6.077,

18 p<0.001) and weight ($n_d=80$, $n_h=27$, Z=-4.770, p<0.001). However, both populations

19 experience sub-optimal access to energy, and consequently maintain minimal levels of

20 body fat and low BMI's (see also Sellen 1999). No significant difference was apparent

21 between the groups in either of these measures (BMI: $n_d=80$, $n_h=27$, Z=-0.269, p=0.788;

22 body fat %: $n_d=79$, $n_h=27$; Z=-0.715; p=0.475), or in age (age: $n_d=80$, $n_h=27$; Z=-1.17,

23 p=0.242).

1   Within each population, men's morning and evening salivary testosterone levels

2   were positively correlated (Datoga: Spearman's ρ=0.322, p=0.006, n=71; Hadza:

3   Spearman's ρ=0.373, p=0.055, n=27), and average testosterone levels were higher in the

4   morning than the evening (Table 1; Datoga: Z=-2.423, p=0.015, n=71; Hadza: Z=-1.727,

5   p=0.084, n=27); however, in the smaller Hadza group these tests fell just short of

6   significance. There were no significant differences between the two populations in either

7   morning or evening measures of salivary testosterone (Figure 2; am: Z=-0.398, p=0.691,

8   n_d=80, n_h=27; pm: Z=-0.294, p=0.769, n_d=71, n_h=27).

9   Among the Hadza, mean age did not differ significantly between fathers and non-

10   fathers (fathers: 38 ± 2.9 yrs, n=10; non-fathers: 31 ± 2.7 yrs, n=15; Z=-1.5, p=0.14).

11   Among the Datoga, mean age was significantly higher for fathers (fathers: 35.5 ± 1.4 yrs,

12   n=48; non-fathers: =24 ± 1.6 yrs, n=30; Z=-5.126, p<0.001). However, there was no

13   relationship between salivary testosterone and age in either population (Datoga am:

14   Spearman's ρ=-0.175, p=0.120, n=80; Datoga pm: Spearman's ρ=-0.094, p=0.434, n=71;

15   Hadza am: Spearman's ρ=-0.154, p=0.442, n=27; Hadza pm: Spearman's ρ=-0.182,

16   p=0.363, n=27).

17   Consistent with data from a range of non-western populations (Bribiescas 2001,

18   Ellison 2003), both Hadza and Datoga men maintained low levels of testosterone in

19   comparison to North American men. Morning testosterone levels averaged 151 and 170

20   pmol/L in the Hadza and Datoga respectively. The same testosterone assay conducted in

21   the same laboratory revealed average morning levels of testosterone in American men

22   from 250 to more than 400 pmol/L, depending on the population sampled (Burnham et al.

23   2003, McIntyre et al. 2003).

1   Among the Datoga, fathers with children under 11 in their homesteads showed no

2   significant difference from non-fathers in either morning (fathers: 166 ± 15.5 pmol/L,

3   n=48; non-fathers: 176 ± 18.5 pmol/L, n=32; Z=-0.629, p=0.53) or evening (fathers: 141

4   ± 12.9 pmol/L, n=41; non-fathers: 138 ± 16.7 pmol/L, n=30; Z=-0.116, p=0.907)

5   measures of testosterone (Figure 3). Mean testosterone levels in polygynously married

6   Datoga men were lower than those of monogamously married men, but this difference

7   was not significant in either morning (polygynous: 142 ± 32 pmol/L, n=12;

8   monogamous: 174 ± 18 pmol/L, n=36; Z=-1.19, p=0.234) or evening samples

9   (polygynous: 93 ± 28 pmol/L, n=9; monogamous: 170 ± 39 pmol/L, n=32; Z=-1.8,

10   p=0.068).

11   Among the Hadza, by contrast, fathers currently caring for children exhibited

12   significantly lower levels of testosterone than men not caring for children in both

13   morning (fathers: 124 ± 13.6 pmol/L, n=10; non-fathers: 176 ± 17.7 pmol/L, n=15; Z=-

14   02.164, p=0.03) and evening samples (Figure 4; fathers: 83 ± 8.83 pmol/L, n=10; non-

15   fathers: 157 ± 16.3 pmol/L, n=15; Z=-2.691, p=0.007). Including two expectant Hadza

16   men in the "father" group (as per Storey et al. 2000, Berg & Wynne-Edwards 2001) had

17   no significant effect on the Hadza father/non-father comparisons (am with expectant

18   fathers: Z=-2.44, p=0.015; pm with expectant fathers: Z=-2.416, p=0.016; n_f=12, n_{nf}=15).

19   Among the ten Hadza fathers currently caring for offspring, age of the youngest

20   child was negatively and significantly correlated with the median percentage decrease in

21   salivary testosterone from morning to evening (Figure 5; Spearman's ρ=-0.659, p=0.024,

22   n=10). This was not the case for Datoga fathers (Spearman's ρ=0.064, p=0.704, n=38).

23

Discussion

1 Previous studies of non-western populations have revealed inconsistent

2 associations between men's testosterone levels and paternal or marital status. We

3 hypothesized that, consistent with the challenge hypothesis, much of this variation can be

4 attributed to differential investment in mating vs. parenting effort, even among married

5 fathers. Our cross-cultural data support this idea by showing that among the Hadza, a

6 group exhibiting high levels of paternal involvement, men caring for offspring maintain

7 lower levels of testosterone than men who are not engaged in such care. By contrast,

8 Datoga fathers, who exhibit low levels of paternal involvement, maintained levels of

9 testosterone similar to those of non-fathers. To our knowledge this is the first

10 demonstration that increased levels of parental care are directly associated with low

11 testosterone in fathers.

12 The Hadza data are particularly interesting because they represent the first

13 examination of testosterone and reproductive effort in a foraging population, where direct

14 paternal care is known to be higher than in many socioecological contexts, including

15 agricultural and industrial societies (Hewlett 1991, Hewlett et al. 2000). Among foragers

16 like the Hadza, when they are not out of camp foraging, men are often near their children,

17 sometimes babysitting weanlings while mothers forage. Because men sleep together with

18 their wives and children, they have direct physical contact with younger children

19 throughout the night. This sort of intimacy is the likely context within which human

20 paternal investment evolved. The increased rates of polygyny and diminished paternal

21 involvement of pastoralists like the Datoga are probably driven by wealth inequalities

1   among men in the form of cattle ownership that would have been absent prior to the

2   domestication of herd animals.

3   The role of fathers in Hadza childrearing is often overlooked, because of the focus

4   on grandmothering in this group (Hawkes et al. 1997). However, in Marlowe's (2005)

5   data, genetic fathers held their children and interacted with their children twice as much

6   as maternal grandmothers. The intensity of care by genetic fathers may be responsible for

7   the relatively robust effects reported here, with morning testosterone in fathers 30%

8   lower, and evening levels almost 50% lower than non-fathers. By contrast, in several

9   North American studies, testosterone differences between fathers and non-fathers were

10   less prominent, and in some cases – particularly among morning samples – non-

11   significant (Berg & Wynne-Edwards 2001, Gray et al. 2002, Gray et al. 2004).

12   A number of studies have reported that evening testosterone levels in humans and

13   chimpanzees show stronger correlates with behavioral measures than do morning samples

14   (Berg & Wynne-Edwards 2001, Gray et al. 2002, Worthmann & Konner 1987, Muller &

15   Wrangham 2004). This pattern may be widespread because morning testosterone levels

16   reflect physiology during sleep, whereas evening samples are influenced by the

17   cumulative outcomes of diurnal social interactions. In the present study we found

18   significant differences between fathers and non-fathers in both morning and evening

19   samples, but in evening samples the magnitude of the disparity was greater, and the p-

20   value lower.

21   Evidence for a suppressive effect of interactions with offspring on testosterone

22   comes from the correlation between age of the youngest child and the relative diurnal

23   decline in testosterone observed in Hadza fathers. Although the sample size is small, the

1   data support the idea that, within populations, the level of direct paternal involvement

2   with offspring affects short-term testosterone production, and that this phenomenon is not

3   limited to a brief period following parturition (Storey et al. 2000).

4   Because of the cross-sectional and correlational nature of our data, however, we

5   cannot entirely rule out the possibility that men with high testosterone levels are less

6   likely to care for young children. Nine of the 15 Hadza men in our "non-father" category

7   had biological children, but were not providing for them, and had terminated relations

8   with the mother. High testosterone levels in these men may have increased the probability

9   of separation from the mother, and one might expect that significant variation exists

10 among men in the degree to which they are responsive to the suppressive effects of infant

11 stimuli. Similar variation might also exist among Datoga men, but would not be

12 detectable given their generally low levels of interaction with children. Longitudinal data

13 are needed to address this critical issue, and these should be available from the Hadza in

14 the near future.

15   Why should testosterone levels be reduced in men caring for young children? As

16 with male birds, it seems likely that testosterone facilitates reproductive effort in the form

17 of male-male competition and mate-seeking behavior, both of which interfere with

18 effective paternal care. Experimental studies in humans have shown that testosterone

19 enhances responsiveness to social challenges (van Honk et al. 1999, van Honk et al.

20 2001, Benderlioglu et al. 2004, Hermans et al. 2008), which can result in a lower latency

21 to reactive aggression in high testosterone men (Kouri et al. 1995). A low threshold for

22 provocation could prove costly in the context of childcare, not only because it might

23 involve men in aggressive interactions with other men, but because it could potentially

1 lead to child abuse, such as infant battering. Although we are not aware of any studies

2 specifically linking androgens to the physical abuse of children, high testosterone in men

3 has been implicated in spousal abuse (Soler et al. 2000).

4   Mate-seeking behavior is also likely to conflict with paternal investment.

5 Increased opportunity for extra-pair matings has been shown to decrease paternal care in

6 birds (Magrath & Elgar 1997), and Marlowe (1999b) documented a similar effect among

7 Hadza fathers, who spend less time caring for and interacting with their children when

8 staying in camps with a larger number of fecund women. Experimental data have shown

9 that men's testosterone levels increase in response to interactions with potential mating

10 partners (Roney et al. 2003, Roney et al. 2007), and this is a plausible mechanism for

11 calibrating men's mating effort to local socioecological conditions. The role of

12 testosterone in promoting libido (Isidori et al. 2005), and the specific association between

13 testosterone and extra-pair mating interest (McIntyre et al. 2006) are consistent with this

14 model. The fact that men's testosterone levels appear to be suppressed in response to

15 infant cues is a strong indicator of the importance of pair bonding and paternal care in

16 human evolutionary history, despite a multi-male, multi-female, fission-fusion social

17 system that promotes opportunities for extra-pair mating.

18

1 **References**

2

3 Archer, J. 2006 Testosterone and human aggression: an evaluation of the challenge

4 hypothesis. *Neurosci. Biobehav. Rev.* **30**, 319-345.

5

6 Beletsky, L. D., Gori, D. F., Freeman, S. & Wingfield, J. C. 1995 Testosterone and

7 polygyny in birds. In *Current Ornithology*, vol. 12 (ed. D. M. Power), pp. 1-42. New

8 York: Plenum Press.

9

10 Benderlioglu, Z., Sciulli, P. W. & Nelson, R. J. 2004 Fluctuating asymmetry predicts

11 human reactive aggression. *Am. J. Hum. Biol.* **16**, 458-469.

12

13 Berg, S. J. & Wynne-Edwards, K. E. 2001 Changes in testosterone, cortisol, and estradiol

14 levels in men becoming fathers. *Mayo Clin. Proc.* **76**, 582-592.

15

16 Blurton Jones, N. C., Smith, L. C., O'Connell, J. F., Hawkes, K. & Kamuzora, C. L. 1992

17 Demography of the Hadza, an increasing and high density population of savanna

18 foragers. *Am. J. Phys. Anthropol.* **89**, 159-181.

19

20 Blystad, A. & Rekdal, O. B. 2003 Datoga. In *Encyclopedia of Medical Anthropology:*

21 *Health and Illness in the World's Cultures*, vol. 2 (ed. C. R. Ember & M. Ember), pp.

22 629-38. New York: Kluwer Academic/Plenum Publishers.

23

1   Booth, A. & Dabbs, J. 1993 Testosterone and men's marriages. *Soc. Forces* **72**, 463-477.

2

3   Borgerhoff Mulder, M. 1992 Demography of Pastoralists: Preliminary Data on the

4   Datoga of Tanzania. *Hum. Ecol.* **20**, 383-405.

5

6   Bribiescas, R. G. 2001 Reproductive ecology and life history of the human male. *Yearb.*

7   *Phys. Anthropol.* **44**, 148-176.

8

9   Brown, R. E., Murdoch, T., Murphy, P. R. & Moger, W. H. 1995 Hormonal responses of

10   male gerbils to stimuli from their mate and pups. *Horm. Behav.* **29**, 474-491.

11

12   Burnham, T. C., Flynn Chapman, J., Gray, P. B., McIntyre, M., Lipson, S. F. & Ellison,

13   P. T. 2003 Men in committed, romantic relationships have lower testosterone *Horm.*

14   *Behav.* **44**, 119-122.

15

16   De Ridder, E., Pinxten, R. & Eens, M. 2000 Experimental evidence of a testosterone-

17   induced shift from paternal to mating behaviour in a facultatively polygynous songbird.

18   *Behav. Ecol. Sociobiol.* **49**, 24-30.

19

20   Ellison, P. 2003 Energetics and reproductive effort. *Am. J. Hum. Biol.* **15**, 342-351.

21

22   Ellison, P. T., Bribiescas, R. G., Bentley, G. R., Campbell, B. C., Lipson, S. F., Panter-

23   Brick, C. & Hill, K. 2002 Population variation in age-related decline in male salivary

testosterone. *Hum. Reprod.* **17**, 3251-3253.

Flinn, M. V., Baewald, C., Decker, S. & England, B. 1998 Evolutionary functions of neuroendocrine response to social environment. *Behav. Brain Sci.* **21**, 372-374.

Gray, P. B. 2003 Marriage, parenting, and testosterone variation among Kenyan Swahili men. *Am. J. Phys. Anthropol.* **122**, 279-286.

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.

Gray, P. B., Ellison, P. T. & Campbell, B. C. 2007 Testosterone and marriage among Ariaal men of northern Kenya. *Curr. Anthropol.* **48**, 750-755.

Gray, P. B., Flynn Chapman, J., Burnham, T. C., McIntyre, M. H., Lipson, S. F. & Ellison, P. T. 2004 Human male pair bonding and testosterone. *Hum. Nat.* **15**, 119-131.

Gray, P. B., Kahlenberg, S. M., Barrett, E. S., Lipson, S. F. & Ellison, P. T. 2002 Marriage and fatherhood are associated with lower testosterone in males. *Evol. Hum. Behav.* **23**, 193-201.

Gray, P. B., Yang, C.-F. J. & Pope, H. G. 2006 Fathers have lower salivary testosterone

levels than unmarried men and married non-fathers in Beijing, China. *Proc. R. Soc. B* **273**, 333-339.

Hawkes, K., O'Connell, J. F. & Blurton Jones, N. G. 1997 Hadza women's time allocation, offspring provisioning, and the evolution of long postmenopausal life spans. *Curr. Anthropol.* **38**, 551-577.

Hegner, R. E. & Wingfield, J. C. 1987 Effects of experimental manipulation of testosterone levels on parental investment and breeding success in male house sparrows. *Auk* **104**, 462-469.

Hermans, E. J., Ramsey, N. F. & Van Honk, J. 2008 Exogenous testosterone enhances responsiveness to social threat in the neural circuitry of social aggression in humans. *Biol. Psychiatry* **63**, 263-270.

Hewlett, B. S. 1991 *Intimate Fathers*. Ann Arbor: University of Michigan Press.

Hewlett, B. S., Lamb, M. E., Leyendecker, B. & Scholmerich, A. 2000 Parental investment strategies among Aka foragers, Ngandu farmers, and Euro-American urban-industrialists. In *Adaptation and Human Behavior* (ed. L. Cronk, N. Chagnon & W. Irons), pp. 155-178. New York: Aldine de Gruyter.

Hirschenhauser, K. & Oliveira, R. F. 2006 Social modulation of androgens in male

vertebrates: meta-analyses of the challenge hypothesis. *Anim. Behav.* **71**, 265-277.

Isidori, A. M., Giannetta, E., Gianfrilli, D., Greco, E. A., Bonifacio, V., Aversa, A.,
Isidori, A., Fabbri, A. & Lenzi, A. 2005 Effects of testosterone on sexual function in
men: results of a meta-analysis. *Clin. Endocrinol.* **63**, 381-394.

Kaplan, H. 1997 The evolution of the human life course. In *Between Zeus and the
Salmon: The Biodemography of Longevity* (ed. K. W. Wachter & C. E. Finch), pp. 175-
211. Washington D.C.: National Academy Press.

Kaplan, H., Hill, K., Lancaster, J. & Hurtado, A. M. 2000 A theory of human life history
evolution: Diet, intelligence, and longevity. *Evol. Anthropol.* **9**, 156-185.

Klima, G. 1970 *The Barabaig: East African Cattle-Herders*. Prospect Heights, IL:
Waveland Press.

Kouri, E. M., Lukas, S. E., Pope, H. G. & Oliva, P. S. 1995 Increased aggressive
responding in male volunteers following the administration of gradually increasing doses
of testosterone cypionate. *Drug Alcohol Depend.* **40**, 73-79.

Lancaster, J. B. & Kaplan, H. 1992 Human mating and family formation strategies: the
effects of variability among males in quality and the allocation of mating effort and
parental investment. In *Topics in Primatology*, vol. 1 (ed. T. Nishida, W. C. McGrew, P.

1   Marler, M. Pickford & F. B. M. de Waal), pp. 21-33. Tokyo: University of Tokyo Press.

2

3   Lipson, S. F. & Ellison, P. T. 1989 Development of protocols for the application of

4   salivary steroid analyses to field conditions. *Am. J. Hum. Biol.* **1**, 249-255.

5

6   Magrath, M. J. L. & Elgar, M. A. 1997 Paternal care declines with increased opportunity

7   for extra-pair matings in fairy martins. *Proc. R. Soc. B* **264**, 1731-1736.

8

9   Marlowe, F. 1999a Male care and mating effort among the Hadza. *Behav. Ecol.*

10   *Sociobiol.* **46**, 57-64.

11

12   Marlowe, F. 1999b Showoffs or providers? The parenting effort of Hadza men. *Evol.*

13   *Hum. Behav.* **20**, 391-404.

14

15   Marlowe, F. 2000 Paternal investment and the human mating system. *Behav. Processes*

16   **51**, 45-61.

17

18   Marlowe, F. W. 2003a The mating system of foragers in the standard cross-cultural

19   sample. *Cross-Cult. Res.* **37**, 282-306.

20

21   Marlowe, F. 2003b A critical period for provisioning by Hadza men: Implications for pair

22   bonding. *Evol. Hum. Behav.* **24**, 217-229.

23

1 Marlowe, F. W. 2005 Who tends Hadza children? In *Hunter-Gatherer Childhoods:*

2 *Evolutionary, Developmental and Cultural Perspectives* (ed. B. S. Hewlett *&* M. E.

3 Lamb), pp. 177-190. New Brunswick: Transaction.

4

5 Marlowe, F. W. In press *The Hadza: Hunter-Gatherers of Tanzania*. Berkeley, CA:

6 University of California Press.

7

8 Mazur, A. & Michalek, J. 1998 Marriage, divorce, and male testosterone. *Soc. Forces* **77**,

9 315-330.

10

11 McIntyre, M., Gangestad, S. W., Gray, P. B., Flynn Chapman, J., Burnham, T. C.,

12 O'Rourke, M. T. & Thornhill, R. 2006 Romantic involvement often reduces men's

13 testosterone levels - but not always: The moderating role of extrapair sexual interest. *J.*

14 *Pers. Soc. Psychol.* **91**, 642-651.

15

16 McIntyre, M. H., Lipson, S. F. & Ellison, P. T. 2003 Effects of developmental and adult

17 androgens on male abdominal adiposity. *Am. J. Hum. Biol.* **15**, 662-666.

18

19 Muller, M., den Tonkelaar, I., Thijssen, J. H. H., Grobbee, D. E. & van der Schouw, Y. T.

20 2003 Endogenous sex hormones in men aged 40-80 years. *Eur. J. Endocrinol.* **149**, 583-

21 589.

22

23 Muller, M. N. & Wrangham, R. W. 2001 The reproductive ecology of male hominoids. In

1   *Reproductive Ecology and Human Evolution* (ed. P. T. Ellison), pp. 397-427. New York:

2   Aldine.

3

4   Muller, M. N. & Wrangham, R. W. 2004 Dominance, aggression and testosterone in wild

5   chimpanzees: A test of the "Challenge Hypothesis". *Anim. Behav.* **67**, 113-123.

6

7   Murdock, G. P. & White, D. R. 1980 Standard cross-cultural sample. In *Cross Cultural*

8   *Samples and Codes* (ed. H. Barry & A. Schlegel), pp. 3-43. Pittsburgh, PA: University of

9   Pittsburgh Press.

10

11   Nunes, S., Fite, J. E. & French, J. A. 2000 Variation in steroid hormones associated with

12   infant care behaviour and experience in male marmosets (*Callithrix kuhlii*). *Anim. Behav.*

13   **60**, 857-865.

14

15   Peters, A., Cockburn, A. & Cunningham, R. 2002 Testosterone treatment suppresses

16   paternal care in superb fairy-wrens, *Malurus cyaneus*, despite their concurrent investment

17   in courtship. *Behav. Ecol. Sociobiol.* **51**, 538-547.

18

19   Reburn, C. J. & Wynne-Edwards, K. E. 1999 Hormonal changes in males of a naturally

20   biparental and a uniparental mammal. *Horm. Behav.* **35**, 163-176.

21

22   Roberts, R. L., Zullo, A., Gustafson, E. A. & Carter, C. S. 1996 Perinatal steroid

23   treatments alter alloparental and affiliative behavior in prairie voles. *Horm. Behav.* **30**,

576-582.

Rodseth, L., Wrangham, R. W., Harrigan, A. M. & Smuts, B. B. 1991 The human community as a primate society. *Curr. Anthropol.* **32**, 221-254.

Roney, J. R., Lukaszewski, A. W. & Simmons, Z. L. 2007 Rapid endocrine responses of young men to social interactions with young women. *Horm. Behav.* **52**, 326-333.

Roney, J. R., Mahler, S. V. & Maestripieri, D. 2003 Behavioral and hormonal responses of men to brief interactions with women. *Evol. Hum. Behav.* **24**, 365-375.

Sellen, D. W. 1999 Growth patterns among seminomadic pastoralists (Datoga) of Tanzania. *Am. J. Phys. Anthropol.* **109**, 187-209.

Sellen, D. W. 1999 Polygyny and child growth in a traditional pastoral society: The case of the Datoga of Tanzania. *Hum. Nat.* **10**, 329-371.

Soler, H., Vinayak, P. & Quadagno, D. 2000 Biosocial aspects of domestic violence. *Psychoneuroendocrinology* **25**, 721-739.

Storey, A. E., Walsh, C. J., Quinton, R. L. & Wynne-Edwards, K. E. 2000 Hormonal correlates of paternal responsiveness in new and expectant fathers. *Evol. Hum. Behav.* **21**, 79-95.

1

2 Trivers, R. L. 1972 Parental investment and sexual selection. In *Sexual Selection and the*

3 *Descent of Man, 1871-1971* (ed. B. Campbell), pp. 136-179. Chicago: Aldine.

4

5 Van Cauter, E. 1990 Diurnal and ultradian rhythms in human endocrine function: a

6 minireview. *Horm. Res.* **34**, 45-53.

7

8 van Honk, J., Tuiten, A., Hermans, E., Putman, P., Koppeschaar, H., Thijssen, J.,

9 Verbaten, R. & van Doornen, L. 2001 A single administration of testosterone induces

10 cardiac accelerative responses to angry faces in healthy young women. *Behav. Neurosci.*

11 **115**, 238-242.

12

13 van Honk, J., Tuiten, A., Verbaten, R., Hout, M. v. d., Koppeshaar, H., Thijssen, J. &

14 Haan, E. d. 1999 Correlations among salivary testosterone, mood, and selective attention

15 to threat in humans. *Horm. Behav.* **36**, 17-24.

16

17 Vermeulen, A., Goemaere, S. & Kaufman, J. M. 1999 Testosterone, body composition

18 and aging. *J. Endocrinol. Invest.* **22**, 110-116.

19

20 Wingfield, J. C., Hegner, R. E., Dufty, A. M. & Ball, G. F. 1990 The "challenge

21 hypothesis": theoretical implications for patterns of testosterone secretion, mating

22 systems, and breeding strategies. *Am. Nat.* **136**, 829-846.

23

1   Wingfield, J. C., Jacobs, J. D., Tramontin, A. D., Perfito, N., Meddle, S., Maney, D. L. &

2   Soma, K. 2000 Toward an ecological basis of hormone-behavior interactions in

3   reproduction of birds. In *Reproduction in Context* (ed. K. Wallen & J. E. Schneider), pp.

4   85-128. Cambridge, MA: MIT Press.

5

6   Woodburn, J. 1968 Stability and flexibility in Hadza residential groupings. In *Man the*

7   *Hunter* (ed. R. B. Lee & I. DeVore), pp. 103-110. Chicago: Aldine.

8

9   Worthman, C. M. & Konner, M. J. 1987 Testosterone levels change with subsistence

10   hunting effort in !Kung San men. *Psychoneuroendocrinology* **12**, 449-458.

1   **Fig. 1** Father-infant proximity by subsistence mode. Data are from the Standard Cross-

2   Cultural Sample (n=139; Murdock & White 1980). The scale from the SCCS is: 1 = no

3   close proximity, 2 = rare instances of close proximity, 3 = occasional or irregular close

4   proximity, 4 = frequent close proximity, 5 = regular, close relationship or companionship.

5

6   **Fig. 2** No significant differences were apparent between the two populations in either

7   morning (p=0.691) or evening (p=0.769) measures of salivary testosterone.

8

9   **Fig. 3** Datoga fathers with children in their homesteads showed no significant difference

10   from non-fathers in either morning (p=0.530) or evening (p=0.907) measures of salivary

11   testosterone.

12

13   **Fig. 4** Hadza fathers currently caring for children exhibited 30% lower levels of

14   testosterone in the morning (p=0.031) and 47% lower levels of testosterone in the

15   evening (p=0.007) than men not caring for children.

16

17   **Fig. 5** Hadza fathers caring for younger offspring showed a larger decrease in salivary

18   testosterone from morning to evening than fathers with older children (Spearman's ρ=-

19   0.659, p=0.024).

20

21

22   **Short Title:** Involved fathers have lower testosterone

1

Table 1 Comparison of anthropometric measures and salivary testosterone (T) levels in

the Hadza and the Datoga.

4

Variable	Hadza Mean ± S.D.	Datoga Mean ± S.D.	P-value
Age (yrs)	33.4 ± 10.1	31.0 ± 10.9	0.242
Height (cm)	158.4 ± 7.6	170.6 ± 6.9	<0.001
Weight (kg)	49.5 ± 5.9	57.2 ± 7.3	<0.001
BMI	19.7 ± 1.9	19.6 ± 1.8	0.788
Body fat (%)	10.3 ± 3.8	10.9 ± 4.3	0.475
AM T (pmol/L)	150 ± 66	171 ± 105	0.691
PM T (pmol/L)	129 ± 62	140 ± 86	0.769

5

1   **Fig. 1**

2

3
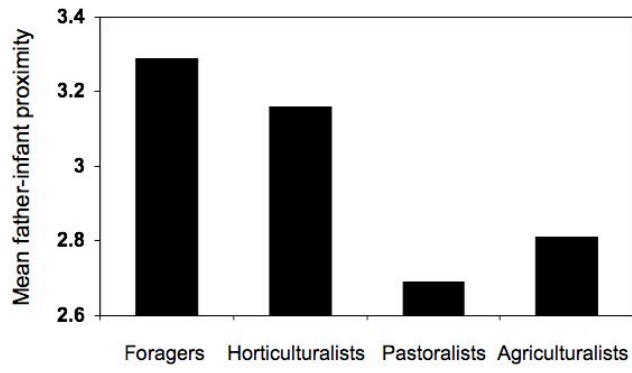
4

5

6

7

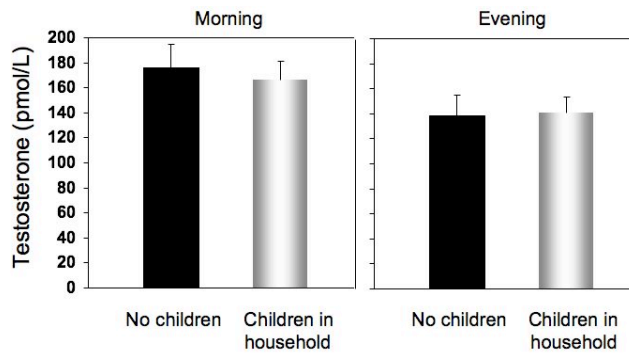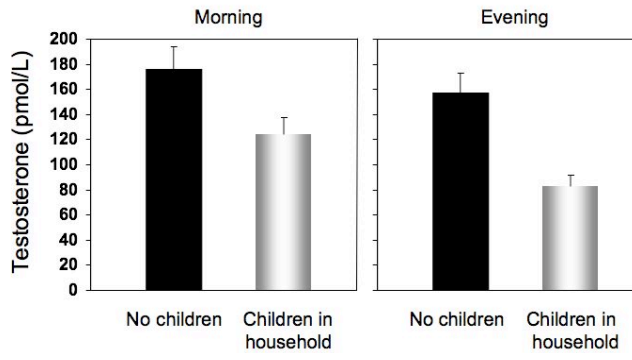1   **Fig. 2**

2

3
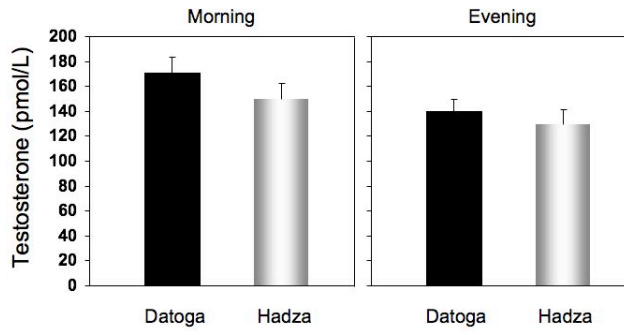
4

1 **Fig 3.**

2

3

4

5

1   **Fig. 4**

2

3

4

5

6

7

8

9

1 **Fig. 5**

2

3

4