

Testosterone positively associated with both male mating effort and paternal behavior in savanna baboons (*Papio cynocephalus*)

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ABSTRACT

Testosterone (T) is often positively associated with male sexual behavior and negatively associated with paternal care. These associations have primarily been demonstrated in species where investment in paternal care begins well after mating activity is complete, when offspring are hatched or born. Different patterns may emerge in studies of species where investment in mating and paternal care overlap temporally, for instance in non-seasonal breeders in which males mate with multiple females sequentially and may simultaneously have multiple offspring of different ages. In a 9-year data set on levels of T in male baboons, fecal concentrations of T (fT) were positively associated with both mate guarding (“consortship”) – a measure of current reproductive activity – and with the number of immature offspring a male had in his social group – a measure of past reproductive activity and an indicator of likely paternal behavior. To further examine the relationship between T and potential paternal behavior, we next drew on an intensive 8-month study of male behavior, and found that fathers were more likely to be in close proximity to their offspring than expected by chance. Because male baboons are known to provide paternal care, and because time in proximity to offspring would facilitate such care, this suggests that T concentrations in wild male baboons may be associated with both current reproductive activity and with current paternal behavior. These results are consistent with the predicted positive association between T and mating effort but not with a negative association between T and paternal care; in male baboons, high levels of T occur in males that are differentially associating with their offspring.

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Introduction

Testosterone (T) is an androgenic steroid hormone, primarily secreted in the testes but also in the adrenal glands, that contributes to the development of secondary sexual characteristics in male vertebrates. T often enhances or is positively associated with mating effort (e.g., Dixon, 2012; Hirschenhauser and Oliveira, 2006; Holekamp and Smale, 1998; Wingfield et al., 1990). It has also been reported to be negatively associated with parental care in some species, particularly monogamous species or those with seasonal breeding schedules (e.g., Alvergne et al., 2009; Brown et al., 1995; Gettler et al., 2011; Ketterson and Nolan, 1999; Reburn and Wynne-Edwards, 1999; Wingfield et al., 1990; Ziegler et al., 2009; reviewed in Magrath and Komdeur, 2003; Stiver and Alonzo, 2009).

Negative associations between T and paternal care are most commonly seen in species in which paternal care involves direct care behaviors such as incubation, infant carrying and provisioning (e.g., in birds:

Lapland longspurs, Hunt et al., 1999; house sparrows, Stoehr and Hill, 2000; European starlings, Pinxten et al., 2007; in fish: Knapp et al., 1999; mammals: gerbils, Brown et al., 1995; black tufted-ear marmosets, Nunes et al., 2001). As noted above, many of these species are also quite seasonal in their breeding, so that they exhibit mating effort and paternal effort at different times. This may allow males to invest intensively in mating effort at one time period without compromising paternal care in another time period.

In contrast, some studies have found a positive association between T and parental care, and still others have found no association at all. Accumulating evidence demonstrates diverse situations in which T is positively associated with paternal effort (e.g. Dwarf hamster (*Phodopus campbelli*): Reburn and Wynne-Edwards, 1999; cotton-top tamarins (*Saguinus oedipus*): Ziegler and Snowdon, 2000; Verreaux's sifaka (*Propithecus verreauxi*): Brockman et al., 2001; California mouse (*Peromyscus californicus*): Trainor and Marler, 2001; redfronted lemur (*Eulemur fulvus rufus*): Ostner et al., 2008; ursine colobus (*Colobus vellerosus*): Teichroeb and Scotte, 2008; Mongolian gerbil (*Meriones unguiculatus*): Juana et al., 2010; Barn swallow (*Hirundo rustica erythrogaster*): Eikenaar et al., 2011). For instance, high T levels are not incompatible with parental care if those elevated levels coincide

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with paternal aggression in defense of the offspring (e.g. Brockman et al., 2001; Juana et al., 2010; Ostner et al., 2008; Reburn and Wynne-Edwards, 1999; Teichroeb and Sicotte, 2008; Ziegler and Snowden, 2000). More generally, the extent to which T is negatively associated with paternal care may depend on the nature of the care that is provided (e.g., providing indirect care may be more compatible with high T than providing direct care; see discussions in Gettler et al., 2011; Gray, 2011; Gray and Campbell 2009; Muller et al., 2009).

Savanna baboons, *Papio cynocephalus*, the subjects of the present study, reproduce throughout the year and offspring experience a protracted period of immaturity. These features mean that baboons provide an excellent example of a species in which males may simultaneously engage in intensive mating effort to obtain access to females and in protection of their own offspring. Aggressive tactics are a pronounced feature of male competition for access to mates. Male baboons compete intensively to acquire and maintain high dominance rank, which enhances their access to potential mates (reviewed in Ellis, 1995), and once a male has access to a mate, he must guard the female from rival males, potentially foregoing foraging or incurring serious injuries or even death (Drews, 1996; Kitchen et al., 2005).

Paternal effort is generally more subtle in baboons and other Old World monkeys than it is in their New World counterparts (Whitten, 1987). Although caretaking in Old World monkeys sometimes consists of infant carrying and defense of immature offspring during agonistic interactions, arguably the most common form of caretaking involves adult males providing an important “safe zone” for both immature offspring and their mothers by maintaining proximity to them (Altmann, 1980; Bales, 1980; Borries et al., 1999; Buchan et al., 2003; Itani, 1959; Nguyen et al., 2009; Noë and Sluiter, 1990; Pereira, 1988; Smuts, 1985; Smuts and Gubernick, 1992; Stein, 1984; Taub, 1984). This form of caretaking and the associated subtle affiliative behaviors between particular pairs of adult males and mothers or young sometimes protect both the mother and the immature from stressful interactions such as rough handling, kidnapping, and infanticide (Altmann, 1980; Kleindorfer and Wasser, 2004; Nguyen et al., 2009; Palombit et al., 1997). Accumulating evidence, including accelerated maturation of offspring whose fathers are present in the social group during the offspring's protracted juvenile period (Charpentier et al., 2008), suggests that male primates sometimes improve the fitness of their offspring through such behavior.

We addressed two goals in the present study of male savanna baboons in Amboseli, Kenya. The two goals sought to relate males' level of T to their current mating effort and to their current close association with their offspring. This required linking results from a long-term data set in goal 1 with a more intensive 8-month data set in goal 2. In goal 1, we determined whether T was correlated with a male's current mating effort or with the number of immature offspring he currently had in his social group. To pursue this first goal we used a long-term data set spanning 9 years of data on T concentrations, mating effort (measured as engagement in mate guarding or “consortships”) and paternity records, while controlling for the effect of factors that has been demonstrated to influence T in our study population: age, dominance rank, seasonal differences in availability of ecological resources. It is well known in primates that individual differences in T may arise from differences in age (e.g. Beehner et al., 2009; Dabbs, 1990; Kaufman and Vermeulen, 2005), social status (Muller and Wrangham, 2004), or ecological factors, such as changes in resource availability (e.g. Cameron et al., 1993; Sapolsky, 1986; Smith et al., 1975). Each of these three factors is also well known to predict T concentration in Amboseli baboons (age: Beehner et al., 2009; Altmann et al., 2010; dominance rank: Gesquiere et al., 2011b; seasonal differences in rainfall: Gesquiere et al., 2011a). It is important to account for such factors that influence levels of T in order to gain a more holistic picture of the relationship between T and reproductive effort.

Second, in goal 2, we used an 8-month intensive behavioral study of males to obtain data on association between males and their immature

offspring that were not available in the long-term dataset, which only had data on number of offspring. Specifically, we identified each male's offspring and determined whether the male was in proximity to his own offspring more than expected by chance. If so, this would allow us, in combination with the results from goal 1, to infer a positive relationship between T concentrations and extent of association with offspring.

Methods

Study population and site

Savanna baboons live in multi-male multi-female societies (Altmann, 1980; Melnick and Pearl, 1987). Males leave their group of birth after reaching reproductive maturity whereas females are philopatric, that is, spend their life in their natal group (Alberts and Altmann, 1995; Pusey and Packer, 1987). Our subjects were part of a wild population that has been the focus of a long-term study, the Amboseli Baboon Research Project. All baboons in the study groups are individually identifiable visually and are habituated to the neutral presence of human observers.

In savanna baboons, matings occur mostly during consortships, defined as mate-guarding episodes accompanied by sociosexual behavior such as copulations, grooming, and close proximity between an adult male and a female in estrus (Alberts et al., 1996). These episodes of mate guarding are associated with intense male–male competition for access to the female in estrus.

Male age and dominance rank

We were able to determine the ages of our study subjects because birth dates of males that were born into study groups were known due to a near-daily visitation of each study group. We estimated ages of immigrant males (those not born into study groups) by comparing their developmental markers to those of individuals with known birth dates (Alberts and Altmann, 1995).

Dominance ranks were calculated for each month based on within-group dyadic agonistic interactions (Hausfater, 1975). We assigned rank 1 to the highest-ranking male, rank 2 to the next in rank and so on.

Seasonal differences in rainfall

Annual precipitation in Amboseli averages 348 mm but is highly variable from year to year, ranging from 150 mm to 550 mm (Altmann et al., 2002). Rains occur almost exclusively from November to end of April or May and as a result this period is wetter than the rest of the year (Alberts et al., 2005). The months of June through October are characterized by a long dry season that is devoid of rain. Here we characterized the months of June–October as belonging to the dry season and the months of November–May as belonging to the wet season.

These seasonal differences in rainfall strongly predict resource availability. For example, individuals have a wide choice of foods during the wet season but resort to so-called fallback foods during the dry season (Alberts et al., 2005). Fallback foods are difficult to process and so animals spend more time foraging and less time resting during the dry season (Alberts et al., 2005). In addition, animals have to travel longer distances between food resources, shade, or water during the dry season than they do during the wet season.

Goal 1: Determining whether (i) current mating effort or (ii) number of immature offspring – a consequence of past mating effort and current opportunity for paternal care – were correlated with fT

This component of the study was based on data collected over a 9-year period, January 2000 to December 2008 and included data

from 96 adult males distributed among 5 study groups. The data included records of demographic, behavioral, and ecological events, and hormonal concentrations for individual males. The ages of the males ranged from 6.2 to 21.7 yrs and their dominance ranks ranged from 1 (highest) to 19 (lowest).

Mating effort: consortship activity

During each visit to a study group, all consortships were identified and the identities of the consort pair were recorded. We extracted this information from our long-term database. These records enabled us to distinguish between males that obtained consortships in any given month (scored as 1) and those that did not (scored as 0). We refer to this measure as mating effort.

Number of immature offspring a male has in his present group

We defined immature individuals as individuals aged 4 years and younger (Buchan et al., 2003). For 277 of 413 immatures (approximately 67%) in the study groups for the 9 years of the long-term component of the study, paternity was determined as described in Alberts et al. (2006). In brief, genetic paternity assignment was based on simple exclusion and also on likelihood-paternity assignment using the program CERVUS (for details see Alberts et al., 2006). Each male's number of immature offspring was determined using these paternity data; immatures for whom paternity had not been determined were dropped from the study. To confirm that this procedure did not result in a biased set of males being considered as fathers, we compared the age and social group distributions of immatures with and without paternity assignments. These two sets of immatures (the ones we analyzed and the ones we dropped, respectively) showed no differences in their birthdate distributions, indicating that having a paternity assignment was random with respect to date of birth. Immatures with no genetic paternity assignment were not completely evenly distributed across social groups; in 4 of the 5 social groups, they represented between ~20% and 30% of the offspring in the study, while in the fifth group they represented 47% of offspring. However, we argue that this deviation in one group was not sufficient to bias our results because (1) unassigned paternities within this group were unbiased with respect to date of birth and (2) we saw no effect of social group in our analysis (see below). Consequently we have no reason to think that the exclusion of immatures with unassigned paternities biased the set of father-offspring pairs we considered.

Fecal sample collection, processing, and testosterone assays

We determined concentration of fT from opportunistically collected fecal samples. We excluded males that had fewer than 5 months in which at least one hormone sample had been collected. Fecal samples are routinely collected as part of the long-term project; methods for fecal sample collection, preservation, and processing have previously been validated (Khan et al., 2002; detailed protocol available at <http://www.princeton.edu/~altlab/AltmannHormoneLabProtocols>). Each fecal sample was collected within a few minutes following observed defecation by a known individual. It was then thoroughly mixed after collection and preserved in vials pre-filled with 95% ethanol to establish an ethanol to fecal sample ratio of approximately 2:1. At the end of each data collection day, fecal samples were stored in an evaporative cooled hut with a daily maximum temperature range of 20 to 25 °C for a maximum of two weeks before they were sent to the University of Nairobi, where the ethanol was evaporated and the samples then freeze-dried. Freeze-dried samples were sifted, weighed to control for dietary differences across seasons and between individuals (Wasser et al., 1993). Steroids were extracted using methanol and subsequently purified using solid phase extraction (using Waters Oasis HLB cartridges, WAT094226) and then kept in a freezer at –20 °C until

assay. Hereafter, we refer to T values we obtained from fecal samples as fT values. For the data presented in this study, concentration of fT, expressed as ng/g fecal powder, was determined as described in Gesquiere et al. (2011a). In brief, we used the Equate ¹²⁵I Testosterone RIA kit (SolidPhase, Portland, ME) beginning in 2000 until its production was discontinued in 2004. At that time, we switched to Diagnostics Systems Laboratories (DSL) 125I Testosterone kit, Beckman Coulter, Webster, TX. These two kits were previously validated for use in our study population (Equate: Lynch et al., 2003; DSL: Beehner et al., 2009). A comparison of fT levels from the two kits using a subset of samples showed a high correlation in fT concentrations ($R^2 = 0.906$, $n = 124$, $p < 0.001$). This enabled us to adjust the levels of samples assayed with the Equate kit, using the equation $T_{DSL} = 1.9676 \times T_{Equate} + 16.9926$, so that the fT concentrations obtained using either kit could be pooled and used in the same analysis (Gesquiere et al., 2011a).

When a male had multiple fT samples in a given month, we used his average fT concentration for that month such that each male had one fT value for each month for which at least one fecal sample was available from that male. The resulting number of months for which hormonal data were available for each male ranged from 4 to 66. Because of other data collection constraints associated with monitoring several hundred individuals of all age-sex classes and the need to collect fecal samples opportunistically, hormonal data were not always available for each male during each month for which the male was studied.

Goal 2: Determining whether the male was in proximity to his own offspring (rather than unrelated immatures) more than expected by chance.

Data used to address this second goal of the study were collected over 8 months, September 2007 to April 2008, when focal sample data were available for adult males. The 37 adult males in our study resided in four social groups. They ranged in age from 7.8 to 18.8 years and in dominance rank from 1 to 14; see Supplementary Material for further details on demography and season for each of the 8 months of data collection on paternal behavior.

We were able to assign genetic paternity to 116 of 118 individuals that were immature during these 8 months; the two immatures with no paternity assignments were excluded from the analysis. As for goal 1, genetic paternity assignment was done following methods described in Alberts et al. (2006).

Measuring proximity between males and their offspring

Male-offspring proximity was scored as nearest neighbor data, and involved recording the identity of the nearest immature within 5 m of the focal male, regardless of whether the youngster was on its own or with other baboons. These data were collected as instantaneous point samples and were recorded at the minute every 2 min during 40 min focal samples (Altmann, 1974). All records were logged into a hand-held computer, the Psion Workabout by Psion Teklogix™. During the 8-month period, the first author observed 37 males for a total of over 395 hrs during 614 focal samples; in all of these samples, the focal male was not in a consortship. The number of focal samples available for each male ranged from 8 to 19.

Data analysis

We used mixed effects models to determine whether mating effort and the number of immature offspring a male had in the group predicted fT (goal 1). Mixed-effects models are suitable for simultaneously dealing with both categorical and continuous predictor variables, pseudoreplication (i.e. repeated measures from the same subject), and uneven number of samples across subjects (Baayen, 2008; Baayen et al., 2008; Crawley, 2007; Pinheiro and Bates, 2000). Mixed effects

models were implemented using the function lmer in the package lme4. We evaluated and selected models based on the Akaike Information Criteria (AIC) such that the final model was the one with the smallest AIC score (Crawley, 2007; Pinheiro and Bates, 2000). Mixed-effects models were performed in the R statistical pack, version 2.9.2.

We used the chi-square goodness of fit test (Sokal and Rohlf, 1995) to determine whether males were more likely to be in close proximity to their immature offspring than would be expected by chance (goal 2).

Goal 1: Do (i) current mating effort or (ii) number of immature offspring predict fT?

The unit of analysis for this goal was male-month, i.e. each month for which hormone data were available for a male. We matched male monthly average fT levels (our response/dependent variable) to the two main fixed effects/predictor variables: mating effort (categorical variable) and the estimated number of immature offspring (continuous) he had in the group that month. In addition to examining the relationship between fT and number of immature offspring, we constructed a categorical variable to enable us compare fT between fathers and non-fathers. Furthermore, for each month, we also identified values of the three potentially confounding factors during that month: age (continuous), dominance rank (ordinal), and season (categorical), which were already well established as predictors of male T in the population. We treated these variables as fixed effects; in total we had five fixed effects. In preliminary analyses we also included average daily maximum temperature in the model, but this variable accounted for no significant variance and so was dropped from the final analysis.

For the random effects structure, we controlled for the effects of both male and group identity. Preliminary data analysis revealed, however, that a model with male identity as the only random effect was a better fit for fT; group differences were associated with very little variance in the model. We thus excluded study group identity from the random effects structure.

Concentrations of fT vary greatly within and among males in our study population. In order to retain between individual differences while avoiding the potential problem of within individual outliers, we excluded, for each male, any fT values that were more than 2 standard deviations above or below that male's mean fT, resulting in the exclusion of 107 values. In total, our remaining data set comprised 2321 male-month fT values.

Goal 2: Were fathers in proximity to their own offspring more than expected by chance?

To address this goal, we restricted the data set to include only those males ($n=21$) that had known genetic offspring and only immatures for whom the genetic father was known ($n=116$). For these males, we (a) examined all the "nearest neighbor" point samples (taken every two minutes) within every focal sample, (b) determined for each point sample whether there was an immature neighbor (each point sample had either 0 or 1 immature neighbor) and (iii) if there was an immature neighbor, scored whether the immature was the focal's offspring or not. In constructing our observed and expected values, we identified the observed and expected number of points in which males had an offspring versus an unrelated immature as a neighbor. In particular, we assigned, to each focal sample (a) F , the count of point samples where the immature neighbor was the focal male's offspring, and (b) N , the count of point samples where the immature neighbor was not the focal male's offspring.

The observed value of males having offspring as neighbors was the total sum of all " F s" across all focal samples, and the observed value of males having unrelated immatures as neighbors as the total sum of " N s" across all focal samples. To calculate the expected value, " $ExpF$ ", of a male having his own offspring as neighbor, we first calculated I_o ,

the proportion of immatures in the group that were a given male's own offspring. We then counted P_i for each focal sample, the total number of point samples during which a male had any immature (offspring or not) as a neighbor. " $ExpF$ " was then $I_o * P_i$, " $ExpN$ ", the expected value of a male having an unrelated offspring as a neighbor was $(1 - I_o) * P_i$. The methods described above are described in more detail in Supplementary Material.

All methods and assay protocols were conducted in accordance with the requirements of scientific research by the Government of Kenya (Research Permit (MOEST 13/001/C351 Vol. II)) and by Princeton University (IACUC 1547).

Results

Goal 1: Did mating effort or number of immature offspring predict fT?

Concentrations of fT were higher in months when males obtained consortships than when they did not (Table 1, Fig. 1). In addition, fT was positively associated with the number of immature offspring a male had in the group; males with more immature offspring had higher fT than those that had fewer immature offspring (Table 1). In other words, fT was positively correlated with both current mating effort and with current opportunities for paternal care. This was true even after controlling for whether the male had any offspring at all (i.e., whether he was a "father" or a "non-father"), and for age and season, the variables that we had previously identified as sources of variance in fT (Altmann et al., 2010; Beehner et al., 2009; Gesquiere et al., 2011a). As before in this population, fT declined with male age, and was higher during the wet than during the dry season (Table 1). We did not find a significant difference in fT between fathers and non-fathers (Table 1).

Male dominance rank and age are strongly correlated in the study population, such that older males tend to be lower ranking. In the present data set, the correlation coefficient, r , was 0.5 between the two variables. Because of this correlation, we further compared the models including only one of these two variables and chose the final model based on how strongly each of the two variables, in addition to the other fixed effects, predicted fT as evaluated by AIC. We found that the model with male age, in addition to the other fixed effects, was a significantly better fit for fT than one with dominance rank, (AIC age vs ranks models = -884.24 vs -840.16 ; $p < 0.001$). Consequently, we re-analyzed the data by excluding dominance rank from the final model and found results that were similar, for the remaining fixed effects, to those shown in Table 1 (see Supplementary Material).

Four different males had 10 or more immature offspring. To investigate the extent to which these exceptionally successful males influenced the relationship between fT and number of immature offspring, we re-ran the analysis excluding these males with 10 or more immature offspring. We found similar patterns as those represented in Table 1: mating effort, $t = 3.47$, $p = 0.0005$; male dominance rank,

Table 1

Multivariate mixed model of log-transformed fT (ng/g): mating effort, number of immature offspring, male dominance, male age, and season significantly predicted differences in fT. Model estimates represent the difference in means of log-transformed fT ng/g (for categorical fixed effects i.e. mating effort, fathers vs. non-fathers, and season) or the change in log-transformed fT ng/g for every unit change in the value of the fixed effect (for ordinal or continuous fixed effects i.e. male age and dominance rank, and a male's number of immature offspring).

| Variable | Estimate | Std. Error | t Value | p Value |
|-------------------------|----------|------------|---------|---------|
| Intercept | 2.251 | 0.041 | 55.46 | 0.0000 |
| Mating effort | 0.028 | 0.009 | 3.30 | 0.0010 |
| Male rank | -0.006 | 0.002 | -3.31 | 0.0009 |
| Number of offspring | 0.008 | 0.003 | 2.88 | 0.0040 |
| Fathers vs. non-fathers | -0.021 | 0.013 | -1.64 | 0.1020 |
| Male age | -0.022 | 0.003 | -7.11 | 0.0000 |
| Season | 0.057 | 0.008 | 7.14 | 0.0000 |

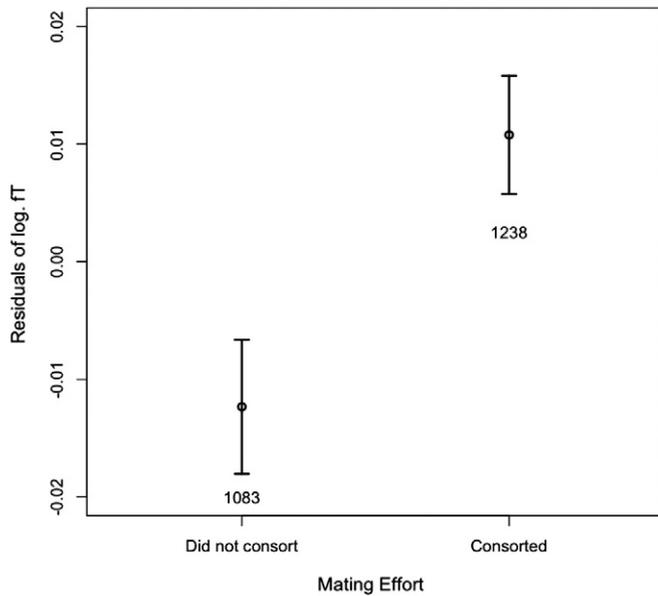


Fig. 1. Concentrations of fT were higher when males consorted than when they did not. Adjusted fT represents residuals after controlling for number of immature offspring, fathers vs. non-fathers, male dominance rank, male age, and season (see text). Points represent means and vertical bars represent standard errors. Number below each error bar represents the number of male-months for each category of mating effort.

$t = -3.28$, $p = 0.0011$; male age, $t = -7.06$, $p < 0.0001$; number of immature offspring, $t = 1.93$, $p = 0.0538$; father vs. non-fathers, $t = -1.40$, $p = 0.1608$; season, $t = 7.08$, $p < 0.0001$. That is, fT was still positively associated with number of immature offspring, although now (with a smaller sample size) p -value was marginally greater than 0.05.

Goal 2: Were fathers in proximity to their own offspring more than expected by chance?

Males had their own offspring as nearest neighbors disproportionately more often than expected ($\chi = 496.36$, $p < 0.001$; see Table 2 and Supplementary Material). In other words, male relationships with immatures were significantly biased toward their own offspring.

Discussion

That T was positively associated with mating effort, as predicted and after controlling for previously investigated variables, is consistent with the intense male competition for access to estrous females that has been demonstrated in several baboon taxa (e.g., Albers et al., 1996, 2003, 2006; Bachmann and Kummer, 1980; Bercovitch, 1983; Bulger, 1993). Consorting male savannah baboons not only display high levels of aggressive behavior but are also recipients of such behaviors as they try to keep rival males from the female consort partner. The higher levels of fT in males who obtained a consort during a given month than in those who did not may be explained by the higher rates of

Table 2

Goodness of fit test to evaluate whether males were more likely than expected to be in proximity to their offspring. Observed values were calculated as the sum of F for offspring and sum of N for non-offspring (see text); Expected values were calculated as the sum of $\text{Exp}F$ for offspring and $\text{Exp}N$ for non-offspring (see text). The data underlying the contingency table are presented in the Supplementary Material.

| Neighbor | Observed (O) | Expected (E) | (O-E) ² /E |
|---|--------------|--------------|----------------------------------|
| Offspring (F) | 483 | 202.17 | 390.09 |
| Non-offspring (N) | 1090 | 1370.83 | 57.03 |
| Chi-square value and associated p value | | | $\chi^2 = 447.62$ $p < 0.001$ |

agonism associated with obtaining consortships, and with high mating activity during these mate-guarding episodes. This result is the first demonstration, to our knowledge, that variation in testosterone levels is associated with variation in mating success after controlling for dominance rank and other relevant variables. However, these results corroborate findings of higher T during periods of higher mating activity, which have been reported for other primates (e.g. ring-tailed lemur: Cavigelli and Pereira, 2000; Gould and Ziegler, 2007; chimpanzees: Muller and Wrangham, 2004; chacma baboons: Beehner et al., 2006; Japanese macaques: Muroyama et al., 2007; redfronted lemur: Ostner et al., 2002, 2008; howler monkeys: van Belle et al., 2009) as well as for non-primate species (e.g. Brown et al., 1995; Goymann et al., 2003; Goymann and Wingfield, 2004; Hegner and Wingfield, 1987; Ketterson and Nolan, 1999; Reburn and Wynne-Edwards, 1999; Wingfield et al., 1990).

In this study, we assessed the relationship between mating effort and fT by comparing fT in months when males engaged in consortship activity with months in which they did not. However, even when males obtain consortships, mating effort may be influenced by several factors including the quality of the reproductive opportunity. For example, males of several nonhuman primates adjust their mating effort based on whether the female consort partner is parous or nulliparous (e.g. mandrills: Setchell and Wickings, 2006; baboons: Gesquiere et al., 2007), on the timing of a consortship relative to ovulation (e.g. baboons: Bulger, 1993; Tonkean macaques: Aujard et al., 1998; chimpanzees: Emery Thompson and Wrangham, 2008), and on whether the female consort partner is experiencing a conceptive or a non-conceptive cycle (e.g. baboons: Bulger, 1993; Gesquiere et al., 2007; chimpanzees: Emery Thompson and Wrangham, 2008). Whether the relationship between mating effort and T depends on differences in the quality of the reproductive opportunity remains an open question for this population.

We demonstrated both a positive relationship between a male's number of immature offspring and his fT (Goal 1), and that males were more likely than expected to be in proximity to their own offspring (Goal 2). In combination, these findings provide support for the emerging understanding that although T may sometimes be antagonistic to paternal care, relatively high T and paternal behavior may co-occur in some species, particularly when production of additional offspring and needs of current offspring are coincident in time. Relatively high T may be compatible with paternal care if paternal care involves aggressive behavior (e.g., Reburn and Wynne-Edwards, 1999), or if paternal care is indirect or limited (e.g., Gettler et al., 2011). We know from our previous findings that male baboons sometimes intervene and defend their offspring against harassment or attacks from conspecifics, both in the Amboseli baboon population (Buchan et al., 2003) and in chacma baboons in which infanticide is a major threat to young (e.g. Palombit et al., 1997). The association between baboon fathers and their offspring demonstrated in the present study may position fathers to aggressively keep away conspecifics that harass or attack the male's immature offspring (examples in baboons include Nguyen et al., 2009). Similar results have been demonstrated in other species of mammals where males exhibit aggressive paternal behavior; in several such species, T has been shown to increase with level of paternal care (e.g. rodents: Dwarf hamster (*P. campbelli*), Reburn and Wynne-Edwards, 1999, Mongolian gerbil, Juana et al., 2010, cf. Brown et al., 1995; primates: some instances in the Verreaux's sifaka, Brockman et al., 2001, redfronted lemur, Ostner et al., 2008, ursine colobus monkeys, Teichroeb and Sicotte, 2008). However, our limited 8-month sample of intensive behavioral data did not allow us to directly test the relationship between fT and the extent to which males actively engaged in paternal behavior.

We further note that spatial relationships between fathers and their immature offspring may be influenced by several factors including the life history stage of the offspring and female reproductive behavior. Consequently, future research on the extent to which such factors

influence paternal behavior in mammals, including nonhuman primates, will greatly improve our knowledge of the patterning of paternal care. For example, additional research is needed to address, firstly, the extent to which changes in offspring age impact the relationship between paternal behavior – including proximity to offspring – and paternal concentrations of T. Secondly, although we used spatial proximity between baboon fathers and their immature offspring as a measure of paternal behavior, such spatial proximity may be influenced by behavior of the offspring's mother when the offspring is very young, and may at that stage partially represent maternal effort rather than paternal effort. As the offspring's dependence on its mother declines, the offspring may itself seek the protection of its father. Furthermore, although spatial relationships between baboon fathers and their immature offspring provide opportunities for fathers to engage in other forms of caretaking (Altmann, 1980; Pereira, 1988; Stein, 1984), these relationships may be initiated by mothers or offspring themselves. Further research is thus needed to disentangle paternal effort from maternal or offspring effort to better understand the relationship between paternal care and T in this species.

The absence of a significant difference in fT between fathers and non-fathers may be attributed to the fact variables that explain variance in T in one category – fathers – may be different than variables that explain T in the other – non-fathers. Furthermore, we note that because we excluded immatures whose genetic fathers are not yet known, the variable fathers vs. non-fathers may not clearly demarcate males based on whether they had offspring or not; the category we are referring to as non-fathers may have included some males with undetected immature offspring.

Taken together, results of the present study lead us to conclude that male baboons, for whom mating behavior and opportunities for paternal care occur simultaneously, must both invest in producing new offspring and caring for existing offspring while experiencing high levels of circulating testosterone. Sources of variability in this relationship and the life history consequences of it remain to be elucidated.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.yhbeh.2012.11.014>.

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