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Endocrinology of year-round reproduction in a highly seasonal habitat: environmental variability in testosterone and glucocorticoids in baboon males

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Abstract

In conditions characterized by energetic constraints, such as in periods of low food availability, some trade-offs between reproduction and self-maintenance may be necessary; even year-round breeders may then be forced to exhibit some reproductive seasonality. Prior research has largely focused on female reproduction and physiology, and few studies have evaluated the impact of environmental factors on males. Here we assessed the effects of season and ambient temperatures on fecal glucocorticoid (fGC) and testosterone (fT) levels in male baboons in Amboseli, Kenya. The Amboseli basin is a highly challenging, semi-arid tropical habitat that is characterized by strongly seasonal patterns of rainfall and by high ambient temperatures. We previously reported that female baboons were impacted by these challenging environmental conditions. We ask here whether male baboons in the same environment and groups as females exhibit similar physiological effects. We found that after accounting for male age and individual variability, males exhibited higher fGC levels and lower fT levels during the dry season than during the wet season. Furthermore, fT but not fGC levels were lower in months of high average daily maximum temperatures, suggesting a direct impact of heat on testes. Our results demonstrate that male baboons, like females, experience ecological stress that alters their reproductive physiology. The impact of the environment on male reproduction deserves more attention both in its own right and because alteration in male physiology may contribute to the reduction in female fertility observed in challenging environments.

Keywords

dry season; food availability; heat stress; fecal hormones; male baboons

Environmental factors can have a dramatic impact on physiology and reproduction (Bronson, 1995). As in many other taxa, some primate species have adapted to seasonal variations in rainfall and food availability by exhibiting strict reproductive seasonality (e.g. tufted capuchin monkeys: Lynch et al., 2002; ring-tailed lemurs: Gould and Ziegler, 2007; Barbary macaques: Menard and Vallet, 1993; northern muriquis: Strier et al., 2001; golden

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lion tamarins: Bales et al. 2006; Verreaux's sifaka: Brockmann et al. 1998; see also Janson and Verdolin, 2005). For some of these species, females are only receptive for a few hours (ring-tailed lemurs: Gould and Ziegler, 2007) to a few days (Verreaux's sifaka: Brockmann et al. 1998) of a short breeding period concentrated in a few months of the year. During the less favorable season, reproductive processes shut down; females stop cycling and males have regressed gonads and low testosterone levels (Brockman et al., 1998; Lynch et al., 2002; Bales et al., 2006; Gould and Ziegler, 2007). Most other primate species reproduce at least occasionally in all months of the year in the wild but still exhibit relatively strong seasonal variability in conceptions and births (e.g. long-tailed macaques: van Schaik and van Noordwijk, 1985; hanuman langurs: Koenig et al., 1997; see Janson and Verdolin, 2005, Table 11.2). At the other extreme from the strictly seasonal breeders are a few species that breed at appreciable frequencies in all months of the year, exhibiting only the slightest seasonal variability. They include examples of new world monkeys (e.g. capuchins, howlers and spider monkeys: Fedigan and Rose, 1995; Strier et al., 2001), old world monkeys (e.g. yellow baboons: Alberts et al., 2005; geladas: Dunbar and Dunbar, 1975; pig-tailed macaques: Oi, 1996), great apes (chimpanzees: Goodall, 1983; gorillas: Watts, 1998) and humans (Ellison et al., 2005) (see also Janson and Verdolin, 2005, Table 11.2 for review).

Seasonal peaks in conception and birth often result from seasonal variability in energetic constraints (review in Bronson, 1995, see also Bailey et al., 1992). Available energy resulting from food consumption first must satisfy requirements associated with an individual's survival such as cellular maintenance, thermoregulation and foraging for food. Growth, reproduction and non-foraging behavior are given lower priority. In periods of low food availability, available energy may be insufficient for both self-maintenance and reproduction, and some trade-offs may be necessary (Hau, 2001; Whitten and Turner, 2009). Ellison and colleagues found that during periods of low food availability women of a population living in Central Africa, the Lese, experience impaired reproductive function such as decrease in the frequency of ovulation, lower estrogen and progesterone levels, and longer intervals between menstruations (Ellison et al., 1986; Bailey et al., 1992; Bentley et al., 1998). These alterations in reproductive pattern were associated with a decrease in body weight in the Lese women. Attainment of menarche and termination of post-partum amenorrhea, two other important transitions leading to successful reproduction in humans, are delayed when resources are limited (Worthman et al., 1993; Riley, 1994; see also review by Bronson, 1995, and Cameron, 1996). Effects of food availability on reproduction have also been documented in some nonhuman primates (e.g. Hanuman langur: Koenig et al., 1997; Long-tailed macaques: van Schaik and van Noordwijk, 1985, Orangutans: Knott, 2005; see also chapters in Brockman and van Schaik, 2005).

The impact of energetic constraints may be further exacerbated by adverse ambient temperatures due to the cost of thermoregulation. High ambient temperatures affect female reproductive function by slowing sexual maturation, decreasing ovulation frequency, and increasing embryo mortality (Bronson, 1989). Low ambient temperatures can also affect primate reproduction, particularly at high latitudes or altitudes, e.g. in chacma baboons at high latitudes by increasing their inter-birth intervals (Hill et al., 2000) and increasing their cortisol levels (Weingrill et al., 2004), and in gelada monkeys at the high altitudes of the Simien mountains by reducing their birth rate (Ohsawa and Dunbar, 1984).

Effects of both ambient temperature and food availability on reproduction are, in part, mediated by steroid hormones. In the presence of a stressor, the hypothalamic-pituitary-adrenal (HPA) axis is activated, and glucocorticoids are secreted by the adrenals. Glucocorticoids activate processes necessary for the mobilization of energy and inhibit processes non essential for immediate survival such as growth, reproduction and immune function. Glucocorticoids decrease the secretion of several hormones of the hypothalamic-

pituitary-gonadal (HPG) axis such as gonadotropin-releasing hormone (GnRH) and luteinizing hormone (LH), leading to a decrease in essential reproductive steroid hormones such as estrogens and testosterone (Collu et al., 1984). However, when the increase in glucocorticoids arises from the demands of mating, the reproductive system sometimes exhibits insensitivity to the action of glucocorticoids. An individual may then exhibit both elevated glucocorticoid and testosterone levels (Lynch et al. 2002; review by Bercovitch and Ziegler, 2002).

In contrast to the large body of information on the impact of environmental factors on female reproduction, few studies have evaluated the impact of environmental factors on male reproductive physiology in species that exhibit only minimal seasonal variability in reproduction, and almost all have been conducted in humans (see review by Bribiescas, 2001). Results from the studies in men have produced less clear results than for women. Under moderate energetic stress, male testosterone levels were not impacted while under similar conditions female reproductive hormones were strongly affected (Garrel et al., 1984; Bentley et al., 1993; Ellison and Panter-Brick, 1996). These authors suggested that the relative insensitivity of male testosterone levels to energy status may reflect the lower investment in reproduction by males as compared to females.

Under very extreme conditions, however, several studies have suggested that male testosterone levels are associated with energy status. For example, experimental studies found that testosterone levels declined after complete fasting both in male rhesus monkeys (Wahab et al., 2008) and in men (Cameron et al., 1993). Similar results were found for Indian men that were naturally experiencing severe malnutrition (Smith et al., 1975) and for adolescent and adult wild baboons during an extreme drought (Sapolsky, 1986). In addition, experimental exposure of testes to temperatures at or above body temperature results in a reduction in sperm quantity and quality in a variety of animal species (Kandeel and Swerdloff, 1988; Liu, 2005; Schwalm et al., 2007, see also review by Hansen, 2009). The effect of high temperatures on testosterone levels has only rarely been examined and to our knowledge, only in farm animals and rodents (Magal et al., 1981; Minton et al., 1981; Larsson et al., 1983; review by Gwazdauskas, 1985). These studies found that exposure to 35°C for long period of time (>4 days) led to a decrease in testosterone levels.

Taken together, the limited available evidence suggests that perhaps males of relatively non-seasonal primate species experience environmental impact on reproductive physiology only under very extreme acute or chronic environmental conditions, i.e. only under the equivalent of pharmacological rather than physiological levels of challenge. Here we capitalize on a long-term study of wild baboons in Amboseli, Kenya, to examine this proposition by evaluating the effects of a highly seasonal and challenging habitat on male physiology. The Amboseli basin is a semi-arid tropical habitat that is characterized by high ambient temperatures and low annual rainfall that is highly seasonal (Alberts et al., 2005; Gesquiere et al., 2008). Like humans, baboons in the tropics reproduce throughout the year and exhibit very little seasonality (Altmann, 1980; Bercovitch and Harding, 1993; also see Janson and Verdolin 2005 Table 11.2). Rates of reproduction in the Amboseli study groups are similar to those reported for other baboon populations, and the Amboseli population is at or slightly above replacement value over the several decades of data collection. However, previous findings from our group demonstrate that reproduction in Amboseli baboons is affected by environmental conditions. Over several decades of study, baboons in Amboseli exhibit a slight seasonal birth peak from August to October, corresponding to an increase in conceptions during the wetter season (Alberts et al., 2005). In addition, we recently demonstrated that females had elevated glucocorticoid levels during the dry season and during the hotter months (Gesquiere et al., 2008). Taken together, these studies demonstrate

that environmental conditions experienced regularly in Amboseli are stressful for female baboons and result in alteration of their reproduction.

Male baboons live year-round in the same groups as females. Adult males are double the body size and are socially dominant to all females, readily securing priority of access to food and water resources, and perhaps buffering them from environmental effects on physiology. We ask here whether male baboons exhibit similar environmentally-induced physiological effects that have been previously found for females in the same environment and social groups. To answer this question, we evaluated the effect of the dry season and periods of extreme heat on males' physiology by measuring fecal glucocorticoids (fGC) and testosterone (fT) concentrations. An absence of changes in both fGC and fT levels would indicate that males are more resistant to environmental challenges than females because of physiological or behavioral buffering. In contrast, an increase in fGC and a decrease in fT during the dry season and the hotter months would suggest that male baboons, like females, experience ecological stress that alters their reproductive physiology. This finding would suggest that changes in male as well as female physiology may contribute to the modest seasonal variability in birthrates.

METHODS

Study population

The subjects in the present study were 114 adult male members of five social groups of wild, non-provisioned baboons in the Amboseli basin, Kenya. Individual life-history data have been collected in the study population for almost four decades (e.g. Altmann and Muruthi, 1988; Altmann et al., 2002; Alberts et al., 2005; see www.princeton.edu/~baboon for a complete bibliography and the Amboseli Baboon Research Project, ABRP, data collection Monitoring Guide). Ages of the subjects were based on known birth dates for males born in study groups, or were estimated based on coat condition, degree of scarring, body carriage and canine tooth condition for immigrant males when they first joined the study population (see Alberts and Altmann, 1995 for details). Since late 1999, physiological data have been obtained from known individuals through non-invasive fecal hormone analysis.

Amboseli weather data

The Amboseli basin in Kenya (2°40'S, 37°15'E, 1100m altitude), is a semi-arid short-grass savannah ecosystem located in an ancient lake basin NW of the base of Mount Kilimanjaro. The environment is characterized by a predictable five-month-long dry season, starting in June that is devoid of rain and during which availability of food and drinking water progressively declines. This dry season is followed by a seven-month wetter period in which rainfall is highly and unpredictably variable from month to month. Rainfall is also highly variable across years (ranging from 150mm to 550mm per year, with a mean value of 348mm/year, see Altmann et al., 2002; Alberts et al., 2005), and drought conditions occur when the normal dry season is unpredictably extended at either end by failure of normal rains.

Although air temperature is less variable across months and years than is rainfall, high temperatures and, therefore, the risk of thermal stress is nonetheless greater in some months, and temperature has increased appreciably over the past several decades (Altmann et al., 2002).

Daily records of rainfall and of minimum and maximum temperature (Tmin and Tmax, respectively) were obtained using a rain gauge and min-max thermometer, placed in the shade, at the research field camp that is within 2-17 km of the ranges of the various baboon

groups (Altmann et al., 2002). Analyses were done at the level of a month, using total rainfall and average daily Tmax for each month of the study.

Across the nine years of the present study (January 2000 - May 2008), the mean monthly Tmax was 33.1°C (28.9°C to 37.9°C) and daily Tmax values sometimes exceeded 40°C. Thus, maximum daily air temperatures in the shade were often close to and sometimes exceeded baboons' normal core body temperature of 38°C (Funkhouser et al., 1967). Furthermore, environmental temperature that baboons experience (termed 'perceived environmental temperature' by Hill et al., 2004) will often be considerably above these shade values, depending on microhabitat, sun exposure, humidity, and behavior.

Hormone data

Fecal sample collection, storage, and extraction were as described previously (Khan et al., 2002; Lynch et al., 2003). In brief, immediately after collection of freshly deposited fecal samples from known individuals, these samples were mixed and placed in 95% ethanol, and stored in a charcoal refrigerator (~20-25°C) for no longer than two weeks. After being shipped to the University of Nairobi the samples were freeze-dried, then sifted to remove the vegetative matter, and stored at -20°C. After transport to Princeton University, 0.2 g of fecal powder was extracted into 2 ml 90% methanol using a multipulse vortexer for 30 minutes. Following extraction, samples were further purified using a prepped Oasis cartridge (Waters, Milford, MA) and stored at -20°C. The samples were then assayed for glucocorticoids (fGC) and testosterone (fT) by radioimmunoassay (Gesquiere et al., 2005; Gesquiere et al., 2008; Beehner et al., 2009; full laboratory protocols also available at www.princeton.edu/~baboon). The primary antibody in the Corticosterone kit for rats and mice (ICN Diagnostics, Costa Mesa, CA) cross-reacts with major cortisol metabolites present in baboon feces (Wasser et al., 2000). Inter-assay coefficients of variation were 13.6% and 10.7% (n=49), respectively for a low and high control. Intra-assay coefficients of variation were below 6% for both the low and high control (any duplicate above 15% was re-assayed). fT concentrations were determined using the Equate ¹²⁵I Testosterone RIA kit (SolidPhase, Portland, ME) in samples collected from January 2000 through July 2004. Because the Equate kit was then discontinued, it was necessary to validate a new T RIA using the Diagnostics Systems Laboratories (DSL) ¹²⁵I Testosterone kit (Beckman Coulter, Webster, TX). Results for parallelism, accuracy, and precision with the Equate and DSL T kit are published respectively in Lynch et al. (2003) and Beehner et al. (2009). In addition, we ran a subset of our samples previously assayed with the Equate kit with the DSL kit, in order to confirm that the two kits give comparable T concentrations. Our results showed a strong correlation between the T values obtained by the two different kits ($R^2=0.906$, n=124, p<0.001), but the T levels obtained with the DSL kit were higher than those with the Equate kit. Using the empirically derived linear regression equation ($T_{DSL}=1.9676*T_{Equate}+16.9926$), we transformed the T levels obtained with the Equate kit so that samples analyzed with both methods could be included in the same analysis. The hormone results are expressed as ng/g dry feces.

For this study we used all the fGC and fT data for males eight years and older obtained from January 2000 through May 2008. We had a total of 3885 fecal samples from 114 males. Because fecal samples were collected *ad libitum*, sample numbers were variable across males and months (N=0-8 samples/male/month; some males were not sampled in particular months). Individuals were never sampled more than once per day. For any month with multiple values for a male, the mean of his values for that month was used for analysis. As a result, we had a total of 2182 monthly values across the 114 males, with an average of 19 (range 1 to 67) months per male.

Statistical analysis

To evaluate the effect of rainfall and temperature on fGC and fT levels, a General Linear Mixed Model (GLMM) was constructed for each hormone, fGC and fT, using SPSS 17.0. In each case, baboon identity was entered into the model as a random factor to control for the unequal and unevenly distributed sampling among males. fGC and fT levels were log transformed to approach normality. The predictor variables entered in each model were two categorical environmental variables: season and temperature (see details for both variables below). We also included one continuous variable, age, in each GLMM, as concentrations of these steroids have been shown to vary with age (Sapolsky and Altmann, 1991; Altmann et al., in press).

After evaluating the full model, we focused first on the effects of season and then on the effects of temperature by analyzing the residual values of each hormone, fGC and fT, that were obtained from the GLMM. Residual values were obtained by running the model described above excluding the environmental variable of interest but including subject, age, and the other environmental variable. For example, to examine the effect of season on fGC, the residual fGC values were calculated by entering temperature and age as predictor variables in the GLMM and baboon identity as a random factor. Non-parametric tests were then performed using the residuals of this model as the response variable and season as the predictor variable, with the statistical threshold set at $p < 0.05$.

Predictor Variables: age—For each fecal sample we determined a male's age on the date the sample was collected. Then, for each male we calculated his monthly mean age at sample collection for each calendar month.

Predictor Variables: environmental factors—The 'season' variable divides months into two categories, the 'dry season' or 'wet season'. 'Dry season' corresponded to the five-month-long dry season from June through October while the 'wet season' included the other seven months from November through May (see Alberts et al., 2005; Gesquiere et al., 2008).

The 'temperature' variable divides months into two categories, 'cool' or 'hot'. Using the daily record of maximum temperatures (T_{max}) over the 101 study months, we calculated a monthly mean T_{max} for each month and considered a month as being 'hot' when its mean T_{max} was above the 3rd quartile T_{max} ($>34.4^{\circ}\text{C}$), otherwise the month was considered 'cool' (see also Gesquiere et al., 2008).

RESULTS

Factors contributing to variation in fGC

Season significantly predicted fGC concentrations in the overall GLMM, whereas temperature and male age did not (Table 1). In our analysis of residuals, adult male fGC concentrations were significantly higher during the dry season than the wet season (Mann-Whitney U: $Z = -3.142$, $p = 0.002$; Fig. 1a), but did not vary with air temperature (Mann-Whitney U: $Z = -0.783$, $p = 0.434$; Fig. 1b).

Factors contributing to variation in fT

Both season and temperature significantly predicted fT concentrations in the overall GLMM (Table 1). In addition, fT levels declined with age of subject ($b = -0.0457$, $p < 0.001$). Our analysis of residuals showed that adult male fT concentrations were significantly lower during the dry season than the wet season (Mann-Whitney U: $Z = -7.927$, $p < 0.001$; Fig. 1a) and were significantly lower during the hotter months than in cooler months (Mann-Whitney U: $Z = -2.320$, $p = 0.020$; Fig. 1b).

DISCUSSION

The physiology of male baboons was clearly impacted by life under the challenging environmental conditions in Amboseli, as previously reported for females (Beehner et al., 2006; Gesquiere et al., 2008). Both fGC and fT levels exhibited differences between dry and wet seasons; residual fGC levels were 2.6 times higher during the dry season, and residual fT levels were 2.6 times lower during the dry season. High ambient temperatures were associated with residual fT levels that were 5.4 times lower than in cooler months. This effect was apparently independent of the HPA axis as fGC did not significantly increase in hotter months.

Seasonality

Male fGC levels were higher during the dry season, when food availability is lower, suggesting that Amboseli baboons seasonally experience energetic stress. As the dry season progresses, baboons in Amboseli switch their diet from easily processed food sources such as grass blades, grass seedheads and shrub/forb leaves to lower profitability fallback foods such as grass corms, which require considerably longer processing time (Post, 1981; Altmann, 1998; 2009; Alberts et al., 2005). The baboons also increase their energetic expenditure, spending more time foraging and less time resting as both food and water become more scarce and patchy (Post, 1981; Alberts et al., 2005; Gesquiere et al., 2008). Both reduction in food intake and increase in energetic expenditure contribute to a reduction in the baboons' energy balance in the dry season. In addition, during the dry season or drought in Amboseli, the baboons' body condition also appears to deteriorate (SCA and JA personal observation and unpublished data), consistent with the physiological findings presented here that male nutritional status is affected during the dry season. When energy reserves are limited, necessary trade-offs occur between energy allocated to self-maintenance and energy allocated to reproduction (Hau, 2001; Whitten and Turner, 2009). Previous studies on wild nonhuman primates have reported effects of energetic constraints on glucocorticoids in males under extreme conditions such as drought (e.g. Sapolsky, 1986 for olive baboons) but not generally otherwise (e.g. Bergman et al., 2005 for chacma baboons; but see Muller & Wrangham, 2004 for high urinary cortisol when both fruit availability was low and aggression levels were high in wild chimpanzees).

Our findings that male baboons had lower levels of the reproductive hormone fT during the dry season are striking. Although energetic impact on male reproductive physiology has not often been investigated, the limited available research on men and male nonhuman primates has reported impact only under extremely severe conditions (see introduction). A decrease in T levels may result in part from the inhibitory action of GC on the HPG axis but peptide hormones such as leptin and insulin may also be involved (reviewed by Schneider, 2004). Peptide hormones cannot be evaluated from fecal sources, and urine samples cannot be obtained from the study population, precluding assessment of those contributors.

Because T has an important role in spermatogenesis, decreases in fT levels such as those observed during the dry season in male baboons might impact male fertility. For example, seasonal changes in testosterone were correlated with changes in sperm quantity and quality in coyotes (Minter and DeLiberto, 2008). However, T may impact behavior more than sperm production in year-round breeding primates such as baboons or humans. T affects male reproductive behavior (such as courtship and aggressive behavior; see review by Wingfield et al., 1990), and even small reductions in fT levels may lead to a reduction in male mating effort and may thereby have consequences for male baboon reproduction.

Ambient temperature

Ambient temperatures also affected male baboon reproductive physiology; fT levels were lower in hotter months. This effect appears to be independent of glucocorticoids, as fGC levels were not higher in hotter months. High ambient temperatures can directly impact testes without activation of the HPA axis as occurs in cryptorchidism, in which the undescended testes are chronically exposed to the higher temperatures within the body. Experimental exposure of testes to elevated temperatures affects spermatogenesis and reduces sperm quality (Kandeel and Swerdloff, 1988; Liu, 2005; Schwalm et al., 2007). However, T levels are only rarely measured in studies of high temperatures. Although several studies have investigated the effect of high temperatures in farm animals and rodents (Magal et al., 1981; Minton et al., 1981; Larsson et al., 1983; see also review by Hansen 2009), we know of no studies of nonhuman primates and only one report focusing on humans (Dabbs, 1990). That study showed that T levels in men are lower during spring and summer than in other months. Ambient heat may also act indirectly as a stressor through the elevation of hormones other than GC, such as the peptide hormone, prolactin (Krulic et al., 1974; Ronchi et al., 2001). Experimental hyperprolactinemia has been reported to decrease T secretion in rats (Huang et al., 1999).

The absence of an increase in fGC in male baboons in hotter months was somewhat surprising as GC has been reported to increase in mammals experimentally exposed to acute ambient temperatures (reviewed in Johnson and Vanjonack, 1975; Gwazdauskas, 1985). However, chronic heat exposure induces a transient rise of GC followed by a return to pre-stress levels through negative feedback, in spite of continued heat treatment. The absence of persistent GC elevation in chronic heat stress is thought to be a thermoregulatory protective mechanism that prevents further metabolic heat production in a hot environment (review in Marai et al., 2002). Male baboons in Amboseli are generally exposed to very hot ambient temperatures for several consecutive weeks; the lack of fGC increase in the male baboons during hotter months may be explained by a return to pre-stress levels through negative feedback mechanisms. If so, why did we find an effect of heat on fGC for baboon females (Gesquiere et al., 2008)? Could male baboons be less sensitive to thermal stress than females? Gender differences in reaction to heat stress have been shown in humans (Frye and Kamon, 1981). Men have lower surface area relative to body mass than women, which results in men experiencing reduced heat gain from the environment on hot days (Falk, 1998; Anderson et al., 2000). In addition, men sweat more than women do (Mehnert et al., 2002; Hazelhurst and Claassen, 2006). Similar gender differences in thermoregulation may occur in adult baboons as males are approximately double the body size of females (Altmann et al., 1993; Altmann and Alberts, 2005), and adult male baboons thus have much lower surface area relative to body mass than adult females. An alternative and not mutually exclusive explanation is that male baboons may be able to spend more time resting or feeding in the shade than the females if they have lower energetic constraints from their much higher dominance status and feeding priority.

Human reproductive ecology traditionally focuses on variation in female reproductive function in response to environmental challenges. The impact of the environment on male reproduction has often been neglected, in part due to the lower metabolic cost of reproduction in males. This sex difference in costs of reproduction forms the cornerstone of the socioecological model of animal societies, which posits that female distributions are driven by food availability, and male distributions are driven by female availability (e.g. Emlen and Oring, 1977). However, our study suggests that in baboons, environmental challenges impact male physiology. Moreover, this effect is not a simple one driven by the presence of cycling females as has been shown for rhesus macaques (Vandenbergh and Drickamer, 1974). In Amboseli multiple fertile females (in the ovulatory phase of the cycle; Gesquiere et al., 2007) are generally available in each social group in all calendar months,

albeit at somewhat lower levels during some months. For example, during the years of present study, approximately four fertile females per group were present in the dry season and an average of six during the wet season. Nonetheless, more subtle indirect environmental effects through each sex on the reproduction of the other despite year-round reproduction remain an intriguing possibility. Studies of environmental impacts on male reproduction in humans and other primates provide a potentially rich area for future research, both for a more complete understanding of male physiology itself and for explaining the reduced fertility observed in extreme environments, which may not be solely due to reduction in female fertility.

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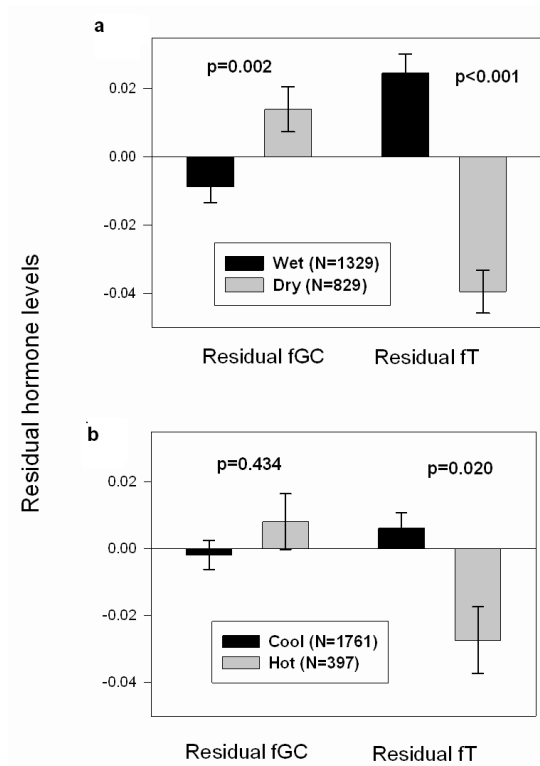


Figure 1.

Differences in fGC and fT concentrations in (a) wet vs. dry season and (b) cool vs. hot months. The y axis represents the residual fGC or fT values obtained from the GLMM, which included all the predictors listed above in Table 1 except for the variable of interest (see Methods). Each value represents the mean \pm SE across male monthly averages. N represents the number of monthly averages. Statistical significance was determined using the Mann Whitney U.

Table 1

Results of GLMM assessing the effect of environmental predictors on fGC and fT concentrations while accounting for age, and with male identity entered as a random factor.

Variables	Numerator df	Denominator df	F	Sig.	b
<i>Dependant variable: log.fGC</i>					
Intercept	1	403.028	4408.16	<0.001	
Age	1	440.887	0.105	0.746	0.0007
Wet/Dry season	1	2093.096	9.085	0.003	-0.0261
Cool/Hot month	1	2105.621	1.116	0.291	-0.0116
<i>Dependant variable: log.fT</i>					
Intercept	1	581.988	3835.386	<0.001	
Age	1	1911.627	238.209	<0.001	-0.0457
Wet/Dry season	1	2051.124	61.714	<0.001	0.0749
Cool/Hot month	1	2055.028	10.778	0.001	0.0396

Significant results appear in bold typeface.