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RESEARCH ARTICLE

Coming of Age: Steroid Hormones of Wild Immature Baboons (*Papio cynocephalus*)

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Large gaps exist in our knowledge about common patterns and variability in the endocrinology of immature nonhuman primates, and even normal hormonal profiles during that life stage are lacking for wild populations. In the present study we present steroid profiles for a wild population of baboons (*Papio cynocephalus*) from infancy through reproductive maturation, obtained by noninvasive fecal analyses. Fecal concentrations of glucocorticoid (fGC) and testosterone (fT) metabolites for males, and of fGC, estrogen (fE), and progestin (fP) metabolites for females were measured by radioimmunoassay (RIA). In males, infancy was characterized by high and declining levels of fGC and fT, whereas steroid concentrations were low during the juvenile years. During the months immediately prior to testicular enlargement, fT (but not fGC) concentration tended to increase. Males that matured early consistently had higher fT and fGC concentrations than those that matured late, but not significantly so at any age. Individual differences in fT concentrations were stable across ages, and average individual fT and fGC concentrations were positively correlated. For females, high and declining levels of fE characterized infancy, and values increased again after 3.5 years of age, as some females reached menarche by that age. Both fP and fGC were relatively low and constant throughout infancy and the juvenile period. During the months immediately prior to menarche, fGC concentration significantly decreased, while no changes were observed for fE levels. fP exhibited a complicated pattern of decrease that was subsequently followed by a more modest and nonsignificant increase as

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menarche approached. Early- (EM) and late-maturing (LM) females differed only in fP concentration; the higher fP concentrations in EM females reached significance at 4–4.5 years of age. Maternal rank at offspring conception did not predict concentrations of any hormone for either sex. Our results demonstrate the presence of individual endocrine variability, which could have important consequences for the timing of sexual maturation and subsequently for individual reproductive success. Further evaluation of the factors that affect hormone concentrations during the juvenile and adolescent periods should lead to a better understanding of mechanisms of life-history variability. Am. J. Primatol. 67:83–100, 2005. © 2005 Wiley-Liss, Inc.

Key words: ***Papio*; infancy; juvenile; sexual maturation; steroids; maternal rank**

INTRODUCTION

The juvenile period remains the least understood primate life stage despite its unusually extended duration and its central position in theories of primate evolutionary history and adaptations [Janson & van Schaik, 1993; Pagel & Harvey, 1993; Pereira, 1993; Pereira & Fairbanks, 1993; Rubenstein, 1993]. The endocrinology of this life stage in wild primates has received even less attention than other topics, such as juvenile behavioral development and growth of body size [Leigh, 1992, 1995; Pereira & Altmann, 1985; Pereira & Leigh, 2003].

Most of the literature on steroid hormone variation during the juvenile period is derived from studies conducted on children [e.g., Angsusingha et al., 1974; Apter, 1980; Elmlinger et al., 2002; Genazzani et al., 1978; Sizonenko, 1989], and several key investigations of captive primates (e.g., baboons [Castracane et al., 1986; Crawford et al., 1997; Muehlenbein et al., 2001], rhesus macaques [Goy et al., 1982; Muehlenbein et al., 2002], and cotton-top tamarins [Ginther et al., 2002]). Large gaps exist in the available literature, and normative data from natural primate populations are virtually absent. Consequently, the extent to which generalizations can be made across human and nonhuman species or from experimental findings on captive primates and unmanipulated wild populations remains unclear, and it is difficult to formulate critical hypotheses.

The present study was undertaken as an initial effort to fill some of these gaps. Our goal was to characterize normative steroid profiles from infancy through reproductive maturation in a well studied baboon (*Papio cynocephalus*) population. This represents a first step toward identifying the relationship of variability in hormones during ontogeny to variability in fitness components. The development of noninvasive techniques [e.g., Khan et al., 2002; Millspaugh & Washburn, 2004; Wasser, 1996; Whitten et al., 1998; Ziegler et al., 1996] has made it possible to investigate steroid profiles of individuals in undisturbed wild populations by measuring excreted products. In this study, we measured fecal glucocorticoid (fGC) and testosterone (fT) metabolites in juvenile males, and fecal glucocorticoid (fGC), estrogen (fE), and progestin (fP) metabolites in juvenile females.

In this study we sought to answer several questions about excreted hormone concentrations in immature baboons in this population: 1) How do hormone concentrations change with age and differ between the sexes? 2) How do hormone

concentrations of individuals change in males and females as sexual maturation approaches? 3) Do early- (EM) and late-maturing (LM) individuals differ in prematurational hormone profiles? 4) Are individual differences in hormone concentrations stable across ages? 5) Does maternal dominance status predict individual differences in offspring hormones?

MATERIALS AND METHODS

Field Site and Subjects

The immature males and females in the present study were members of five social groups in the Amboseli baboon population. Individual life-history data for members of these study groups cover over three decades [e.g., Alberts & Altmann, 1995a,b, 2003; Altmann & Alberts, 2003; Altmann et al., 1988; Pereira, 1988; Shopland, 1987] (see www.princeton.edu/~baboon for a complete bibliography and the Baboon Project Monitoring Guide, which outlines the data collection protocols). The demographic and behavioral records in our database (BABASE) that are relevant to the present investigation include name, sex, birth, group of birth, date of sexual maturation, maternal parity, and maternal dominance rank at the offspring's conception. The maturation date for females is taken as the onset of sex-skin swelling in the first menstrual cycle. For males the date of reproductive maturation is taken as the first day of the first month during which observable scrotal rounding associated with testicular enlargement was recorded in our regular assessments [Alberts & Altmann, 1995b]. For individuals in the present sample, the median age at reproductive maturation (calculated using survival analysis with censored values in Sigma Plot 8.0; SPSS Inc., 2002) was 4.53 years (54.4 months) for females, and 5.27 years (63.2 months) for males.

Collection and Preparation of Fecal Samples

Fecal samples were collected ad libitum for this project beginning in December 1999. A total of 1,552 fecal samples from 69 immature females (6 months to 5 years old) were collected through December 2002, and 1,901 samples for 81 males (6 months to 6 years old) were collected through February 2004. The fecal sample collection, storage, and extraction were performed as described previously [Khan et al., 2002; Lynch et al., 2003]. The female samples were assayed for estrogen (fE), progestin (fP), and glucocorticoid (fGC) metabolites, and the male samples were assayed for testosterone (fT) and fGC metabolites, all by radioimmunoassay (RIA) [Altmann et al., 2004; Khan et al., 2002; Lynch et al., 2003].

Data Analysis

Only the raw data for fE were distributed normally. Therefore, we used a log transformation (base 10) on all of the endocrine data, which produced a normal distribution for the full data set for each hormone and for almost all subsets. Consequently, we use these transformed values for both descriptive statistics (mean and standard error (SE) assuming normality) in a graphical presentation, and parametric statistical tests. All analyses were conducted for 6-month intervals because adequate sampling across individuals for a finer-grained temporal analysis could not be achieved, and analysis at shorter intervals produced a noisier picture.

Population-level analyses. Our data set is a mixed longitudinal-cross-sectional one. For a descriptive account of the population endocrine profile, we first conducted an age-based analysis (by considering the time since birth), and calculated the mean and SE across individuals for each 6-month period. For each 6-month age period, we included only individuals for which we had at least three samples within that period. Multiple samples for an individual during any period were reduced to a single value by using the individual's mean concentration during the period.

To create hormone profiles for the 1.5 years prior to each individual's maturation date, the analysis used each individual's own maturation date rather than its birth date. Consequently, we included only those males and females for which the maturation date was known (i.e., it had already occurred by the time of analysis) and for which data were available for each of the three 6-month periods prior to maturation (n=20 males, n=14 females). In calculating the average population value for each 6-month period prior to maturation, we also calculated a mean concentration for each individual as described above. We used general linear model (GLM) procedures with repeated measures in SPSS 12.0 (SPSS Inc., 2003) to evaluate changes in hormone concentrations across the three time blocks, and we used paired *t*-tests within time blocks.

For both males and females, we conducted a second age-based, population-level descriptive analysis to evaluate differences between EM and LM animals. For this analysis, we categorized individuals that matured before the median age as EM, and those that matured after that age as LM. The few individuals that fell within 2 weeks of the median, and those that could not yet be categorized because they were too young were not included in this analysis. In all, 353 samples for 20 EM females, 638 samples for 19 LM females, 249 samples for 14 EM males, and 477 samples for 15 LM males were available for this analysis. We used a *t*-test to compare EM and LM individuals at any age period.

Analyses to evaluate individual differences in hormone concentrations. To characterize each individual's relative hormone concentrations at any age, and to determine whether relative hormone concentrations represented stable individual traits during the immature years, we calculated each individual's deviation from the average population value at each age. For that purpose we used a common nonparametric locally weighted regression procedure (LOWESS) on the full set of raw values, with a sampling proportion of 0.5 in Sigma Plot 8.0 (SPSS Inc., 2002). The residuals were calculated for each hormone sample as the ratio of the observed to the predicted values (as determined by Sigma Plot). The data were then pooled into four periods to obtain adequate data for individuals for multiple periods while maintaining distinct major stages of development (males: 0.5–3.0 years, 3.0–4.0 years, 4.0–5.0 years, and 5.0–6.0 years; females: 0.5–2.5 years, 2.5–3.5 years, 3.5–4.5 years, and 4.5–5.5 years). A mean residual value was calculated for each baboon for each of these periods. The mean residuals were then logarithm-transformed (base 10) to approximate a normal distribution. Individuals with high concentrations compared to the population as a whole will have positive values of log residuals, and those with relatively low concentrations will have negative ones (see also Moses et al. [1992] and Johnson [2003] for a similar approach to analysis of growth data). We then compared stability across successive ages using linear regression between pairs of periods to test whether an individual's relative hormone concentration at an earlier age significantly predicted its relative value at a later one.

We next evaluated the relationship among hormones within individuals by calculating a single overall value for each individual for each hormone using the

average of its four log residuals values. For females, we then calculated the Pearson correlations between E and P, E and GC, and P and GC. For males we calculated the Spearman Rho correlation between GC and T because the distribution of the individual average log GC values for males were not normal.

Finally, for each hormone we used linear regression to test whether maternal dominance rank at the time of the offspring's conception predicted the immature individual's average hormone concentration.

RESULTS

How Do Hormone Concentrations Change With Age and Differ Between the Sexes?

Males exhibited their highest levels of GC and T metabolites early in infancy (Fig. 1a). Concentrations progressively decreased throughout infancy, reaching their lowest levels by 2 years of age for fGC and early in the third year of life for fT. Concentrations then remained constant during the juvenile period for fGC, but rose at the end of the fourth year of life for fT. Around the average age of testicular enlargement, fT (but not fGC) again increased slightly. This second rise is at least partially attributable to those males that had matured by this age (see following section).

Estrogen concentrations in young females showed a strikingly similar pattern to those of T in young males (Fig. 1b). Estrogen levels decreased during the first 2 years of life, remained stable for the next 1.5 years, and then increased around 3.5 years of age. After 4 years of age, both the mean and the variance in fE increased (seen as an increase in SE; Fig. 1b) because some females had reached menarche (and experienced a surge in fE) by that time, while others had not. For females, both P and GC were relatively constant throughout infancy and the

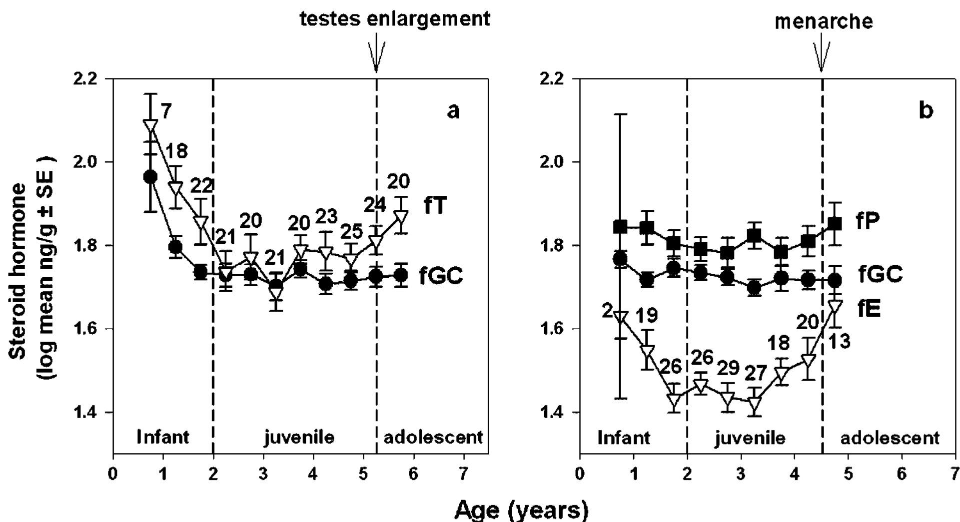

Fig. 1. Endocrine profile across age in (**a**) male and (**b**) female baboons. Each value represents the mean ± SE across individuals of the log-transformed concentration (ng/g feces) of fGC, fT, fE, and fP for a 6-month period. *N*'s represent the number of baboons sampled for each age period. Average age of sexual maturity is indicated for each sex.

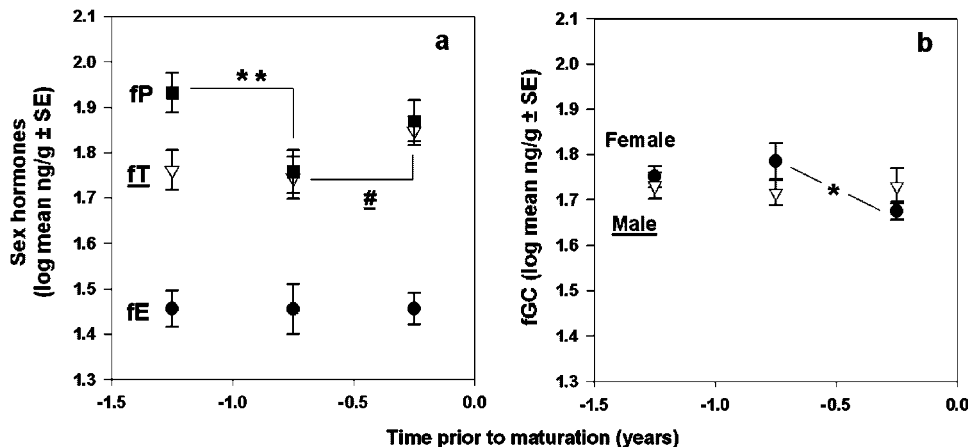

Fig. 2. Endocrine profiles across the 1.5 years prior to maturation for individuals sampled during all three of the 6-month time periods (see Materials and Methods for details). Mean ± SE of (**a**) fT, fE, and fP; and (**b**) fGC in 6-month intervals prior to sexual maturation. Open symbols represent male steroid hormones (n=20), and closed symbols female hormones (n=14). Paired *t*-test: $^{\#}P<0.1$, $^{*}P<0.05$, $^{**}P<0.01$.

juvenile period. During the juvenile years, concentrations of fGC were similar in males and females.

Because sex steroid concentrations around puberty will be highly dependent on the state of an individual (i.e., mature or not mature), we focused next on each individual's hormone levels in relation to its maturation date rather than its birth date (age).

Do Fecal Hormone Concentrations Change in Males and Females Shortly Before They Attain Sexual Maturity?

Progestin concentrations changed significantly during the year and a half prior to maturation ($F_{2,12}=5.276$, $P=0.023$), while fE concentrations did not ($F_{2,12}=0.0$, $P=1.0$) (Fig. 2a). The change in fP resulted from a decrease in concentrations 1.5–1.0 years prior to menarche (1.931 ± 0.161 (mean ± SD) vs. 1.759 ± 0.176, $t_{14}=3.379$, $P=0.005$), and a small and nonsignificant increase just before maturity. Male fT concentrations tended to increase across the full time period ($F_{2,18}=3.257$, $P=0.062$) (Fig. 2a), particularly so during the 6 months immediately preceding maturation (1.745 ± 0.206 vs. 1.849 ± 0.144, $t_{19}=-2.064$, $P=0.053$).

Overall concentrations of GC metabolites were similar for males and females throughout this 1.5-year period (1.726 ± 0.091 vs. 1.738 ± 0.077; $t_{32}=0.379$, $P=0.707$) (Fig. 2b). Nonetheless, female fGC concentrations declined significantly from 1.0 year to 0.5 year prior to maturation ($F_{2,12}=5.537$, $P=0.020$; 1.786 ± 0.149 vs. 1.676 ± 0.074, paired sample $t_{13}=2.517$, $P=0.026$) whereas those for males did not ($F_{2,18}=0.135$, $P=0.874$).

Do EM and LM Juveniles Differ in Prematurational Hormone Profiles?

Males that matured early tended to have higher concentrations of fT (Fig. 3a) and fGC (Fig. 3b) during almost every age period than those that matured late,

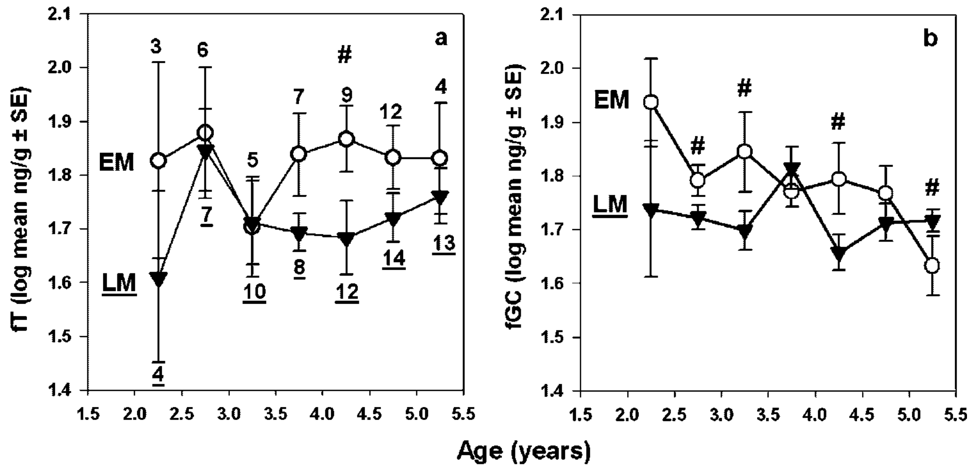

Fig. 3. Comparison of hormone concentrations of (**a**) fT and (**b**) fGC across age in male baboons that matured early or late relative to the population median (see Materials and Methods for details). N's represent the number of males sampled for each age period. Independent t-test: $^{\#}P<0.1$.

and the differences did not reach statistical significance in any time period. EM and LM females did not differ significantly or consistently in either fE or fGC concentrations (Fig. 4a and c). However, P concentrations tended to be higher in EM females compared to LM females at every age (Fig. 4b). This result reached significance when the females were 4.0–4.5 years old ($t_{17}=3.403$, $P=0.003$).

Are Individual Differences in Hormone Concentrations Stable Across Ages?

Relative fT concentration was a stable individual trait in males: those who had high concentrations relative to their peers at early ages also did so at later ages (Table Ia). In contrast, a male's level of fGC at a young age did not predict the levels at subsequent ages, although the slope of the regression from one age to the next was positive in all but one case. Nonetheless, individuals' overall relative fGC and fT values were positively correlated (Spearman's Rho: $R=0.301$, $P=0.007$).

In contrast to males, females showed no stable individual differences in sex steroids. Neither fE nor fP concentrations were predictive across the prematurational period (Table Ib), and even the sign of the slope was variable (not shown). However, possible stability is suggested by the females' fGC levels (Table Ib). For females, individuals' overall hormone concentrations were not correlated (Pearson correlation: $R=0.146$, $P=0.231$ for fE and fP, $R=-0.037$; $P=0.764$ for fE and fGC, $R=0.119$; $P=0.328$ for fP and fGC).

Does Maternal Dominance Status Predict Individual Differences in Offspring Hormones?

Maternal dominance rank at offspring conception did not predict relative fT or fGC concentrations of immature males at any age period (Table IIa), nor did it predict the fE, fP, and fGC concentrations of young females (Table IIb).

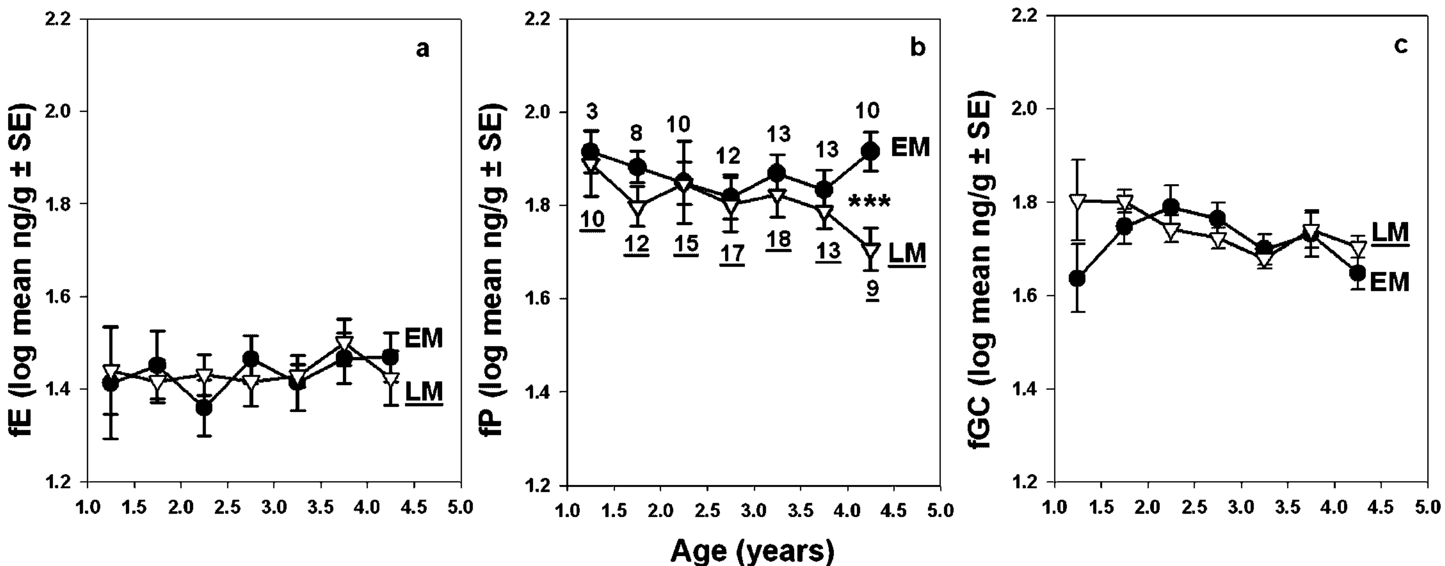

Fig. 4. Comparison of hormone concentrations of (**a**) fE, (**b**) fP, and (**c**) fGC across age in female baboons that matured early or late relative to the population median (see Materials and Methods for details). N's represent the number of females sampled for each age period. Independent t-test: $^{***}P<0.005$.

TABLE Ia. Predicting Male Hormone Concentrations at Each Age Period From Those at the Previous Age Period†

	Subsequent age			
	0.5–3	3–4	4–5	5–6
Log residual fT				
Prior age				
0.5–3	**X**	0.521***	0.496***	0.0007
3–4		**X**	0.358***	0.266*
4–5			**X**	0.18#
5–6				**X**
Log Residual fGC				
Prior age				
0.5–3	**X**	0.028	0.037	0.048
3–4		**X**	0.114#	0.000
4–5			**X**	0.005
5–6				**X**

†Values in each cell represent the R^2 value from an ordinary linear regression analysis.
ANOVA: #$P<0.1$; *$P<0.05$; **$P<0.01$; ***$P<0.005$.

TABLE Ib. Predicting Female Hormone Concentrations at Each Age Period From Those at the Previous Age Period†

	Subsequent age		
	0.5–2.5	2.5–3.5	4–5
E, Log residual fE			
Prior age			
0.5–2.5	**X**	0.017	0.007
2.5–3.5		**X**	0.02
3.5–4.5			**X**
P, Log residual fP			
Prior age			
0.5–2.5	**X**	0.104#	0.05
2.5–3.5		**X**	0.000
3.5–4.5			**X**
GC, Log residual fGC			
Prior age			
0.5–2.5	**X**	0.185*	0.017
2.5–3.5		**X**	0.145#
3.5–4.5			**X**

†Values in each cell represent the R^2 value from an ordinary linear regression analysis.
ANOVA: #$P<0.1$; *$P<0.05$; **$P<0.01$; ***$P<0.005$.

DISCUSSION

Steroid Metabolites During Infancy

Infancy in our baboon population was characterized by high and declining fE concentrations in females, and high fT and fGC concentrations in males.

TABLE IIa. Predicting Male Hormone Levels From Maternal Dominance Rank*

	fT		fGC	
Age period	Slope	R^2	Slope	R^2
0.5–3 years	−0.173	0.03	−0.136	0.019
3–4 years	0.227	0.052	0.099	0.010
4–5 years	−0.208	0.043	−0.059	0.003
5–6 years	−0.010	0.000	−0.166	0.028
Average	−0.062	0.004	−0.141	0.020

*Values in the cells represent the slope and R^2 values from an ordinary linear regression analysis. ANOVA: $P > 0.2$.

TABLE IIb. Predicting Female Hormone Concentrations From Maternal Dominance Rank*

	fE		fP		fGC	
Age period	Slope	R^2	Slope	R^2	Slope	R^2
0.5–2.5 years	−0.019	0.000	−0.036	0.001	0.155	0.024
2.5–3.5 years	0.119	0.0144	−0.130	0.017	0.021	0.000
3.5–4.5 years	0.043	0.002	−0.280	0.078	−0.040	0.002
Average	0.143	0.020	−0.110	0.012	0.132	0.018

*Values in the cells represent the slope and R^2 values from an ordinary linear regression analysis. ANOVA: $P > 0.2$.

A neonatal surge of steroid hormones during the first 2–3 months of life has been reported by many authors (e.g., for boys [Andersson et al., 1998; Kenny et al., 1966; Kiess et al., 1995; Forest et al., 1973], rhesus macaques [Mann et al., 1989; Nevison et al., 1997], marmosets [Dixson, 1986; Lunn et al., 1994; Pryce et al., 2002], and cotton-top tamarins [Ginther et al., 2002]. The period of elevated neonatal androgens in our study may arise if we are measuring metabolites that are of both gonadal and adrenal origin. Adrenal steroid production is significant during infancy. Crawford et al. [1997] reported high levels of the sulfated conjugate dehydroepiandrosterone (DHEA-S) in serum of baboons until about 1.5–2.0 years of age. Furthermore, Möhle et al. [2002] found in macaques that the metabolic products of T and of DHEA were very similar in feces. Therefore, it is possible that the T antibody used in our assays cross-reacts with DHEA metabolites if their chemical structure is similar. Although adrenal production of DHEA may explain elevated fT concentration, it does not explain the higher fE and fGC levels that we also found in infants. Consequently, biological interpretation of our data for infancy remains problematic.

Sex Steroids in the Transition From the Juvenile Period to Sexual Maturation

As maturation approached, somewhat different pictures are provided by the age- and stage-based results. The age-based population profile suggested an increase in sex steroids for the females prior to average age at maturation. A similar increase in reproductive hormones around the average age at puberty has been reported in girls for E and P [Angsusingha et al., 1974; Apter, 1980; Apter & Vihko, 1977; Elmlinger et al., 2002; Genazzani et al., 1978; Nottelmann et al., 1987]. However, this increase was apparently the result of heterogeny of

reproductive state (pre- vs. postmenarche) among females of this age. For individuals examined over the 1.5 years prior to menarche, fE concentrations did not increase. A similar analysis for fP prior to menarche revealed a decrease in concentration in the year preceding menarche. Since the primary source of progesterone before the onset of ovulation is the adrenals, our results could be interpreted as suggesting a decrease in adrenal production of P. This parallels our finding of a decrease in fGC shortly before menarche.

It is more difficult for males than for females to compare our data with those in the literature for this immediate prematurational stage. While menarche is used as an obvious criterion for sexual maturity in females of many primate species, for males there is no obvious or standardized marker to indicate sexual maturity. In the primate literature, the onset of puberty or sexual maturation is reported as the time of testicular descent (e.g., macaques) or enlargement (e.g., humans and baboons), depending on whether the species has testes that are scrotal or inguinal at birth [Castracane et al., 1986; Crawford et al., 1997; Ginther et al., 2002; Muehlenbein et al., 2001, 2002; Nieuwenhuijsen et al., 1987; Nottelmann et al., 1987]. However, both testicular enlargement and descent occur in a gradual fashion. In the literature for captive primates, estimation of testes volume is generally used to quantify testes size; however, estimation methods vary. Furthermore, we cannot yet readily relate our observational criterion of scrotal rounding [Altmann et al., 1977] to any of the volume-estimation methods, although we based it on the findings of Snow [1967], who reported that the period of rapid size increase corresponds to the onset of production of viable sperm. An additional complication is that the endocrine data in the literature were obtained from blood samples that were collected at daytime hours that varied among the different studies. Release of T in early puberty is pulsatile, and higher T concentrations occur at night [Stanhope & Brook, 1988]. Consequently, comparisons among studies are of necessity presently limited. Nonetheless, the increase in fT concentration at the average age of testicular enlargement observed at Amboseli is in general agreement with previous studies of captive baboons [Castracane et al., 1986; Crawford et al., 1997; Muehlenbein et al., 2001], which all found an increase in plasma T concentrations around the time of testicular enlargement. In our analysis of the 1.5 years preceding maturation, we found a near significant ($P=0.053$) fT increase in the 6 months preceding maturation. Marson et al. [1991] reported an increase in serum T prior to testes enlargement in male chimpanzees (*Pan troglodytes troglodytes*), while Nieuwenhuijsen et al. [1987] did not detect any changes in serum T until after testicular descent in stumptail macaques (*Macaca arctoides*). At the present time we cannot determine whether these different results represent biological differences or methodological ones, such as the differences in the times of blood sample collection mentioned above. One advantage of analyzing hormones from fecal samples is the integrative nature of the samples across 1 or more days, resulting in an absence of strong diurnal variations in larger primates [Beehner & Whitten, 2004].

Glucocorticoids Prior to Sexual Maturation: Differences Between Males and Females

In the Amboseli baboons, fGC concentrations decreased prior to menarche for females, but not at the comparable stage for males. The explanation for this may lie in the complex nature and multiple roles of GCs, both in mobilizing energy for the nutritionally more demanding adolescent period, and as a

component of the stress response [Romero, 2004]. Baboon females, like females of many cercopithecine species, have dominance relationships that are very stable throughout adulthood, and a daughter will attain a rank similar to that of her mother. Nonetheless, a female's adult rank does not exist at birth; rather, it is achieved through agonistic encounters during the juvenile years, and rank attainment is usually completed approximately 1 year before menarche [Walters & Seyfarth, 1987] (Altmann and Alberts, unpublished data). As a result, baboon females may experience a reduction in stress levels of GCs in the year prior to menarche that will at least temporarily offset any increase associated with metabolic demands. This suggestion is consistent with the lack of decline in fGC in the males in our study. Metabolic demands increase much more in males than in females because the males (but not the females) experience a large growth spurt in the fourth year of life, and this growth continues for at least 3 years as the males' body mass doubles [e.g., Altmann & Alberts, 2005; Johnson, 2003]. Moreover, although males attain dominance rank over all females during the juvenile years, as they make the transition to adolescence and production of viable sperm they are increasingly targeted aggressively by older males.

Sources of Variability in Juvenile Hormone Concentrations

Age at maturation. Our data contrasting EM and LM individuals are suggestive, albeit preliminary. Although fT concentrations were consistently higher in EM males than in LM males during six of seven time periods, and fGC concentrations were higher during five of seven time periods, the two groups did not significantly differ during any of these periods for either hormone. EM and LM females did not differ consistently or statistically in fE and fGC. However, EM females had consistently higher fP levels than the LM females (seven of seven time periods), and the difference became significant shortly after their fourth birthday. In contrast, Apter and Vikho [1985] reported estradiol levels in humans that were higher in EM girls, while levels of 17-OH progesterone and pregnenolone did not differ between EM and LM girls. Whether estrogen levels are more important for the timing of sexual maturation in humans, and progestin levels are more important in baboons is not clear, nor do we know why this would be the case. However, Strier and Ziegler [2000] found that prior to dispersal, some young muriqui females (*Brachyteles arachnoides*) experienced cycle fluctuations in their progesterone levels, even though they had low, stable estradiol levels. A possible explanation for our data is that the EM female baboons experienced progesterone fluctuations earlier than the LM females, or that the amplitude of the progesterone peaks was greater and therefore more readily detectable in the EM females. An alternative explanation for the increase in progesterone levels in the EM females in the months prior to menarche is that while no sexual swelling was detected, the young females may have started to cycle. This suggests than an increase in progesterone levels may provide an earlier marker of the onset of puberty than the estrogen-based sexual swelling.

Individual differences. Individuals' T concentrations relative to age peers were stable across ages (i.e., they had the characteristics of a stable individual trait, with concentrations at an early age predicting concentrations at a later age). Some individuals had consistently higher fT concentrations, while others had lower fT concentrations throughout the immature years. In contrast, fGC levels were not consistent across time within individuals. These data are similar to those of Bercovitch and Clarke [1995], who reported that adolescent rhesus macaques have stable plasma T concentrations but inconsistent cortisol

concentrations. Nonetheless, among the immature baboons, average fGC and fT were correlated, suggesting a more complex relationship between these two hormones. Previously published studies also indicated that the relationship between T and GC is not consistent. In adult males of several vertebrate species, T and GC are sometimes (but not always) positively associated [Casto et al., 2001; Creel, 2001; Coe et al., 1979; Lynch et al., 2002; Sapolsky, 1986a], and the relationship of each of these hormones to dominance rank is also variable. Comparable data on the relationship between T and GC are not available for juveniles, but exist for captive adolescent nonhuman primates. In a study of adolescent male rhesus macaques (*Macaca mulatta*), the highest-ranking individuals had higher T concentrations at a younger age compared to low-ranking age peers [Bercovitch, 1993], while no difference in cortisol levels was found between low- and high-ranking individuals [Bercovitch & Clarke, 1995]. Cortisol was not inversely correlated with T, as it is in adult males. Our preliminary data on juveniles, combined with the interesting studies on colony adolescents and the variable findings for adults, highlight the need to obtain information (particularly ontogenetic data) at all life stages of an individual, as well as the insights that can be gained from such information. The concentrations of each hormone and the relationships among these hormones are likely to be contingent on a variety of factors, including social and physical environments. These may account for some of the patterns and the as-yet-unexplained variability in our present dataset.

Social and environmental factors. A number of social and environmental factors influence growth and maturation in human and nonhuman primates, and different ones often predominate under different conditions or for different species.

Maternal rank affects both growth rates and age at sexual maturation of the Amboseli males and females [Altmann & Alberts, 2003, 2005; Alberts & Altmann, 1995b; Altmann et al., 1988], and has similar effects in a number of other populations [Bercovitch & Strum, 1993; Johnson, 2003; Wasser et al., 2004]. Moreover, maternal rank has been shown to correlate with serum T levels of captive adolescent sons in rhesus monkeys [Dixson & Nevison, 1997]. However, in a study by Setchell and Dixson [2002] of semi-free-ranging provisioned adolescent male mandrills, dominant males had higher T levels than subordinate males, but dominant males were not necessarily sons of high-ranking females, and maternal rank did not predict T concentrations. In agreement with that study, we found that maternal rank did not predict either T or GC concentrations in immature males, nor did it predict concentrations of steroid hormones in immature females.

The absence of correlation between maternal rank and endocrine status may be due to other confounding factors on which these variables are contingent, such as variation in group size, group composition, or environmental condition. As is the case for other nonhuman primates, social factors influence the age of maturity [Abbott et al., 1990; Bercovitch & Goy, 1990; Graham & Nadler, 1990; Ziegler et al., 1990]. The social environment is also reported to influence the endocrine level. For example, Mendoza and Mason [1991] reported elevated estradiol levels in adult female squirrel monkeys after they were introduced to an adult male, and Goy et al. [1992] found higher T levels in male rhesus monkeys that were housed with three females instead of one. In other studies, the presence of dominant adult or adolescent males depressed the androgens levels of the younger, more subordinate males (mandrills [Wickings & Dixson, 1992], rhesus macaques [Bercovitch, 1993], and orangutans [Maggioncalda et al., 1999]). Environmental factors such as rainfall, temperature, and daylight duration also influence steroid

hormones, as reported for cortisol concentrations [Cavigelli, 1999; Millspaugh & Washburn, 2004; Sapolsky, 1986b; Weingrill et al., 2004].

Variability in foraging conditions also accounts for major differences in both growth and maturation [Altmann & Alberts, 2003, 2005; Strum & Western, 1982]. However, much of the variation in age of maturation still remains to be explained after foraging differences are taken into account, and some of this residual variability may lie in individual differences in endocrinology. In Amboseli, growth rates contributed to age of maturation both directly and through rank-based maternal effects. Like growth differences, hormonal differences may be partially a function of maternal rank, and may in turn make some independent contribution to differences in age of maturation. However, the strength of these effects may be highly contingent on other factors [e.g., Altmann & Alberts 2003, 2005; Bercovitch & Strum, 1993; Bulger & Hamilton, 1987; Wasser et al., 2004] that vary across and within populations. Just as heritability estimates are dependent on the environment of measurement, estimates of factors determining variability in life-history components may differ across studies because they differ across conditions.

The data presented here sketch the outline of steroid changes that occur during ontogeny, and the individual variation in hormone levels and timing of maturation in a wild population. Investigating individual endocrine profiles over time, and further evaluating the factors that affect hormone concentrations during the juvenile and adolescent periods are the next steps in understanding the patterns and variation in maturation in this and other populations. Thanks to the development of noninvasive techniques, it is now possible to conduct fine-grained studies to assess variability under different social and ecological conditions, maturational stage, and species differences. This will enable researchers to answer a host of questions about the mechanisms of life-history variability in natural populations.

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