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RESEARCH ARTICLE

Life-History Correlates of Steroid Concentrations in Wild Peripartum Baboons

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Steroid concentrations during late pregnancy and early lactation may be affected by both a female's reproductive history and her current condition, and may in turn predict subsequent life-history events, such as offspring survival. This study investigated these relationships in a wild primate population through the use of fecal steroid analysis in repeated sampling of peripartum baboons (*Papio cynocephalus*). Fecal samples were collected from 32 females in five groups within the Amboseli basin during 8 weeks prior to parturition and 13 weeks postpartum. From December 1999 through February 2002, 176 fecal samples were collected from individuals representing 39 peripartum periods. Fecal concentrations of progestins (fP), estrogen metabolites (fE), glucocorticoids (fGC), and testosterone metabolites (fT) were measured by radioimmunoassay. Steroid concentrations declined from late pregnancy to lactation, and the decline was greatest and most precipitous for fE and fP. Primiparous females had significantly higher mean fE concentrations in each of the last 2 months of pregnancy compared to multiparous females. Among multiparous females, fE and fT were significantly higher during late pregnancy in females carrying a male fetus compared to those carrying a female fetus. During early lactation, high fT in young mothers predicted subsequent infant death during the first year of life. These findings illustrate the potential power of repeated fecal-steroid sampling to elucidate mechanisms of life-history variability in natural populations. They also document significant differences in hormone profiles among subgroups, and highlight that such normative subgroup information is essential for interpreting

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Key words: *Papio*; pregnancy; lactation; steroids; parity; fetal sex; offspring survival

INTRODUCTION

Parturition is a major life-history event, with fitness consequences for both the mother and the offspring she produces. The peripartum period is of particular significance for mammals, such as primates, that have high levels of investment in both gestation and the postpartum care of offspring. Understanding hormonal profiles of females during this period is central to elucidating the mechanisms of life-history variability in natural populations.

Hormones during pregnancy and lactation have traditionally been studied for humans and a few species of nonhuman primates in captivity. Comparable research in the wild and for a greater diversity of species is now possible thanks to advances in noninvasive techniques that permit steroid collection and analysis without disruption to the animals' daily lives. Such noninvasive approaches are of particular value during this highly sensitive life stage. In this study we extracted hormones from feces to evaluate demographic predictors of variability in peripartum steroid concentrations (estrogens, progestins, glucocorticoids, and androgens) and the life-history sequalae of that variability, for a population of wild-living baboons (*Papio cynocephalus*).

Female Reproductive Hormones and the Effects of Parity

Of the steroid hormones, estrogens and progestins are the ones most commonly associated with the prepartum period in pregnant mammals. They generally increase during late pregnancy and decrease rapidly at parturition. In addition, patterns of hormonal variability may be associated with postpartum maternal behavior and offspring success. Nonetheless, the strength of these temporal changes in hormones and in hormone–behavior relationships may differ among subsets of females in a population. In particular, it has been postulated that a major difference that has been observed between the first and subsequent pregnancies will occur in general because hormones that organize behavior of the primipara subsequently serve as activators during later pregnancies by stimulating previously organized suites of endocrine-mediated behaviors [e.g., Bridges, 1975, 1996]. Here we document the normative pattern of change in fE and fP over the periparturitional period, and test the hypothesis that prepartum concentrations of fE and fP are greater in primipara than in multipara.

Maternal Androgens and Fetal Sex

Androgen concentrations have only rarely been investigated in pregnant nonhuman primates [Altmann et al., 1995; Castracane, 1982; Chambers & Hearn, 1979; Stavisky, 1994]. In humans, serum testosterone increases significantly during the first trimester of pregnancy and continues to rise throughout the pregnancy [Castracane et al., 1992; Fleming et al., 1997a]. Whether differences in fetal sex affect this trajectory during the first half of pregnancy (weeks 4–20) is unclear [cf., Castracane et al., 1992; Glass & Klein, 1981; Klinga et al., 1978]. During the second half of pregnancy (weeks 20–40), however, women carrying a

male fetus have significantly higher serum T than those carrying a female fetus [Meulenberg & Hofman, 1991]. Data on two lemur species revealed that females carrying male fetuses had higher estrogen concentrations during pregnancy than those carrying female fetuses [Shideler et al., 1983; Ostner et al., 2003]. In the present study, we evaluated the extent to which fetal sex predicts fT and fE concentrations during late pregnancy in baboons.

Steroid Hormones and Maternal Success

Studies of glucocorticoids in postpartum women have demonstrated that cortisol concentration is positively associated with affectionate and vocal interaction toward infants [Fleming, 1990], and increased attentiveness to infant-generated cues [Fleming et al., 1997b]. This suggests that increased postpartum glucocorticoid concentrations may enhance maternal behavior or infant survivorship. The limited results from (captive) nonhuman primates are less clear [Bahr et al., 1998; Bardi et al., 2003, 2004]. Here we test the a priori hypothesis that high postpartum cortisol concentrations predict subsequent offspring survival, and evaluate whether the other fecal steroids are predictive of offspring survival.

MATERIALS AND METHODS

Field Site, Study Subjects, and Collection of Demographic and Reproductive Data

The baboons in the present study were members of the Amboseli population. Long-term data are available for this population regarding individual life histories, ecology, and behaviors (see www.princeton.edu/~baboon for a complete bibliography of work on this population). A baboon female usually experiences her first pregnancy during her 6th year of life, and, if she survives, continues to produce a single infant every 2 years for the next 15 years or more. Only rarely does a female cease to reproduce before she dies. Births occur throughout the year and exhibit only slight birth seasonality in Amboseli [Alberts et al., in press; Altmann et al., 1988]. Annual mortality is highest during the first year of life [Alberts & Altmann, 2003], and the mortality rates of adult females are highest in Amboseli during pregnancy and lactation [Altmann et al., 1988].

Data on all demographic events, including births and deaths, are recorded on a near-daily basis in five study groups. Female reproductive status is readily determined from external signals, such as sex skin tumescence and coloration, menstruation, and paracallosal coloration. The full maturational and reproductive history is known for all females in the current study.

Collection, Preservation, and Preparation of Fecal Samples

For fecal samples collected ad libitum during the 27-month period starting in December 1999, we used a subset of 176 samples that were obtained from adult females during their last 8 weeks of pregnancy and first 13 weeks of lactation. The samples also met the following criteria for inclusion: Only pregnancies resulting in live births were included in the analyses of pregnancy, and only samples from those females whose infants survived past 14 weeks of age were included in analyses for the lactational period. These samples span 39 peripartum periods of 32 females, and represent all parities from 1 to 10 (Table I). Freshly deposited fecal samples were collected in vials that were prefilled with 95% ethanol to

TABLE I. Number of Females Sampled During Late Pregnancy and Early Lactation, by Parity for the Sampled Pregnancy and Sex of Offspring From That Pregnancy (See Materials and Methods)

Parity	Pregnancy			Lactation		
	Male offspring	Female offspring	Total	Male offspring	Female offspring	Total
1	3	5	8	2	2	4
2	3	4	7	1	3	4
3	1	2	3	1	2	3
4	1	3	4	0	2	2
5	0	1	1	0	1	1
6	2	2	4	1	1	2
7	2	1	3	2	1	3
8	1	1	2	1	1	2
9	0	1	1	0	1	1
10	1	1	2	1	1	2
Total	14	21	35	9	15	24

approximate a volumetric ratio of 2:5 feces to ethanol. The samples were stored for <1 month at Amboseli, and were then transported to the National Museums of Kenya in Nairobi. There the ethanol was evaporated, and the samples were lyophilized and stored in a -20°C freezer. The dried samples were then transported to Princeton University. Each sample was sifted through fine mesh, and 0.2 g of sample was extracted into 2 ml of 90% methanol. The methanol extracts were subjected to solid phase extraction prior to radioimmunoassay [Khan et al., 2002; Lynch et al., 2003].

Radioimmunoassays

Steroid concentrations of baboon fE, fGC, fT, and fP were assessed by means of I-125 radioimmunoassay. All samples were assayed in duplicate, and mean concentrations were expressed as nanogram of hormone per gram of dry fecal matter [Wasser et al., 1993]. For assay development and validation for fE and fGC (as modified from Wasser et al. [1988, 2000]) see Khan et al. [2002], and for fT and fP see Lynch et al. [2003]. We further validated the testosterone metabolite radioimmunoassay for female baboons by running a female baboon fecal pool through high-performance liquid chromatography (HPLC), using techniques from Strier et al. [1999]. Each 1-min fraction was subsequently assayed to determine cross-reactivity with the testosterone antibody. Cross-reactivity occurred in the fractions with testosterone, as well as with 3b-androstanediol and etiocholanolone, both of which are testosterone metabolites. Further, the testosterone antibody showed no cross-reactivity with cortisol, cortisone, or corticosterone. The intra- and interassay coefficients of variation for the pools were 3.6% and 7.9% for the fE assays (n=6), 3.4% and 7.0% for the fT assays (n=4), 4.9% and 15.8% for the fP assays (n=6), and 6.9% and 9.5% for the fGC assays (n=6).

Data Analyses

Data on maternal parity, dominance rank, date of parturition, offspring sex, and infant survivorship were obtained from BABASE, the electronic long-term database for the Amboseli Baboon Project. Endocrine data were logarithm-

transformed (base 10) to achieve an approximately normal distribution with uniform variance. A populational week-to-week profile of steroid concentrations (fE, fP, fT, and fGC) was then constructed for the last trimester (2 months) of pregnancy and the first 3 months of lactation. Data were divided into 1-week intervals relative to the date of parturition, which was counted as the first day of ''week 1.'' When multiple fecal samples were available from any female from a particular pregnancy for a particular week, we used the mean concentration for that female's samples for that week so that each female contributed only a single value to the population mean for each week for a given birth. This resulted in 143 weekly values.

To analyze predictors and sequalae of variability in steroid concentrations, we divided the data into three periods: two prepartum periods and a single postpartum/lactational period. Pregnancy lasts approximately 25 weeks. For convenience, weeks 5–8 prior to parturition are termed ''month 5 of pregnancy,'' and weeks 1–4 prior to parturition are ''month 6 of pregnancy'' throughout this paper. For these analyses, we took the mean of weekly means for a female if data were available for >1 week of that month, again ensuring that only a single value per female was used in any analysis. Independent-sample t-tests were used to analyze differences by maternal parity, fetal sex, and offspring survivorship. A significance value of 0.05 was used throughout.

RESULTS

Transition From Pregnancy to Lactation

The mean concentrations for all steroids but testosterone metabolites decreased significantly from pregnancy to lactation (fE: $t=23.4$, $P<0.001$; fP: $t=9.9$, $P<0.001$; fT: $t=2.0$, $P=0.063$; fGC: $t=3.2$, $P=0.005$) in paired comparisons for all pregnancies in which the female was sampled during both pregnancy and lactation ($n=20$). The pattern for testosterone was more complex across lactation than that of the other hormones, as can be seen in the weekly profiles (Fig. 1).

The mean weekly steroid concentrations for fE, fP, fT, and fGC were similar across weeks during the 8 weeks prior to parturition when all pregnancies were considered (Fig. 1). Females had a higher steroid concentration of fE, fP, and fGC during the first week of lactation compared to weeks 2–13 of lactation (Fig. 1). For this reason, and because fecal steroids during the first days after parturition are likely to still reflect pregnancy values of circulating steroids, the first week after parturition was excluded from subsequent analyses of the postpartum period.

Parity As a Predictor of Steroid Concentrations

Pregnant primiparous females had significantly higher fE concentrations than pregnant multiparous females in months 5 ($t=2.8$, $df=21$, $P=0.01$) and 6 ($t=3.6$, $df=25$, $P=0.001$) of pregnancy (Fig. 2). The mean concentrations of fP, fT, and fGC did not differ between pregnant primiparous and pregnant multiparous females. During the lactational period (weeks 2–13 postpartum), primiparous and multiparous females did not differ in mean concentrations of any of the four steroids analyzed.

Offspring Sex As a Predictor of Steroid Concentrations

We restricted our analysis of offspring sex to multiparous females because we had identified (see above) some significant prepartum hormonal differences

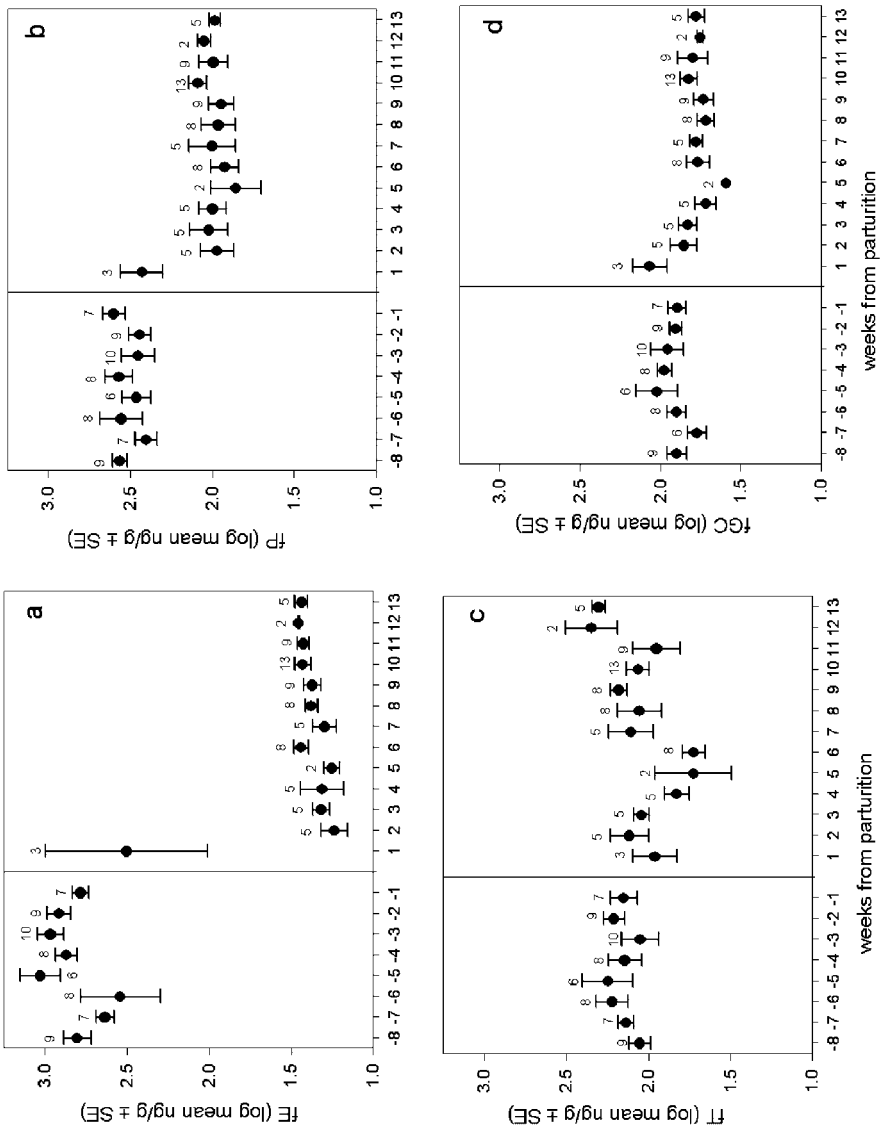

Fig. 1. Mean concentrations of log-transformed (a) fE, (b) fP, (c) fT, and (d) fGC ng/g feces ± SE by week from parturition. n = the number of females sampled in each category.

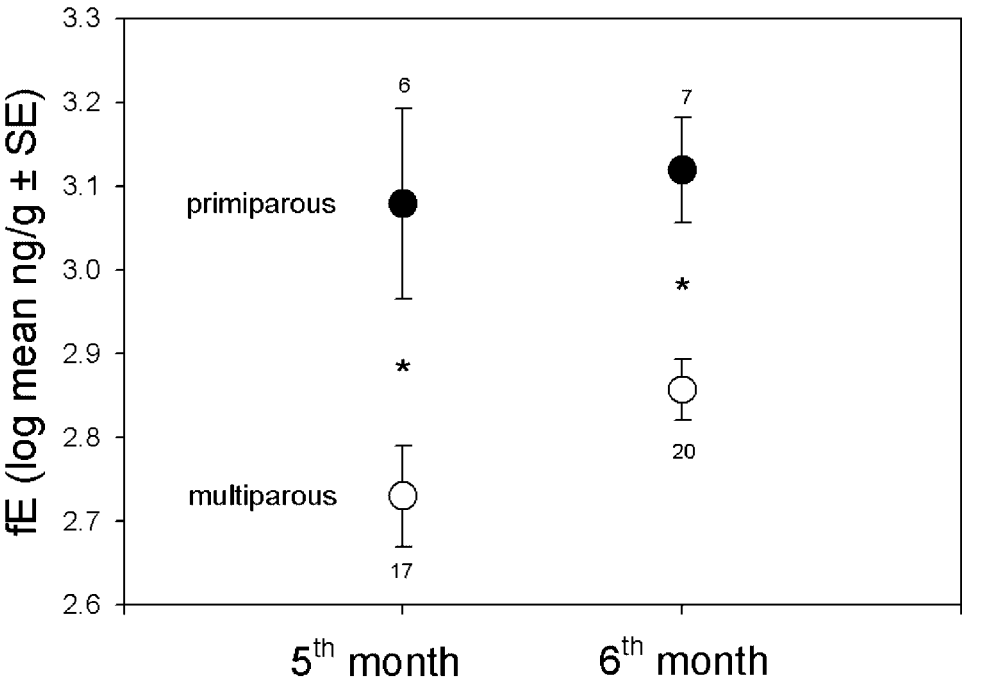

Fig. 2. Mean fE concentrations for primiparous and multiparous females in months 5 and 6 of pregnancy.

between multiparous and primiparous females, and too few primiparous females were sampled at the appropriate times for us to examine the effects of offspring sex in this group. For the pregnancies of eight multiparous females, samples were available for months 5 and 6 of pregnancy, as well as during lactation. Four of these pregnancies resulted in male offspring, and four resulted in female offspring. The two subsets did not differ with respect to maternal parity or dominance rank. Multiparous females with male fetuses tended to have higher concentrations of all four hormones in all three periods, particularly so during late pregnancy (Fig. 3a–d). Despite the small number of individuals involved, this difference reached statistical significance during late pregnancy for fT concentrations during month 5 ($t=2.8$, $P=0.03$), and for fE during month 6 ($t=3.5$, $P=0.013$).

Predicting Offspring Survivorship

Of the infants from this study that survived beyond the first 3 months of life, the only ones that died within the first year of life were born to females of low parity (parity=1–3). Consequently, in evaluating hormonal predictors of offspring survival, we avoided confounding differences in parity by using only those 12 females (eight females with infants that survived to 1 year, and four with infants that died) with a parity of <4. Mothers whose infants subsequently died had a higher mean fT during the first 3 months postpartum compared to those whose infants survived the remainder of the first year of life (mean 2.23 ± 0.0775 SE vs. 1.87 ± 0.0814 (all values $\log_{10}$ as described in Materials and Methods); $t=2.7$, $df=10$, $P=0.021$). Concentrations of fGC, fE, and fP during the first 3 months postpartum did not predict subsequent offspring survival.

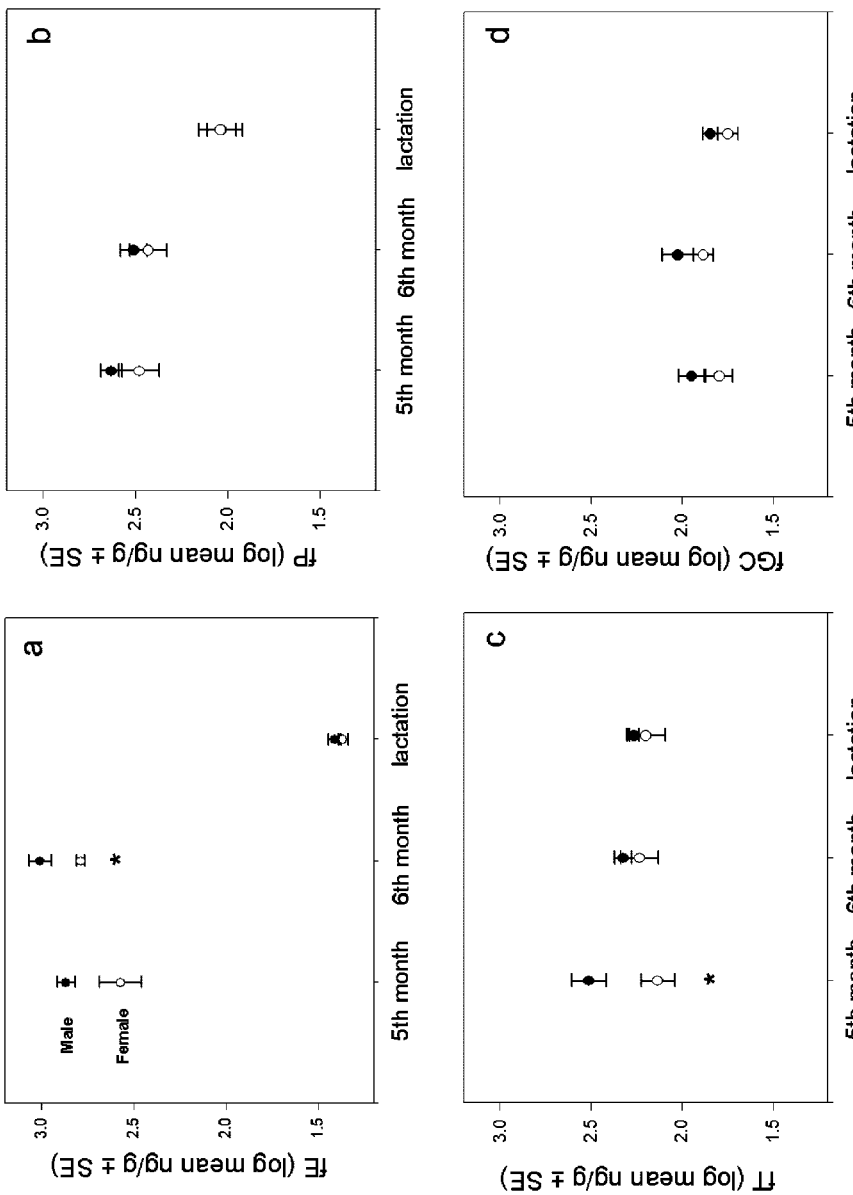

Fig. 3. Mean (a) fE, (b) fP, (c) fT, and (d) fGC concentrations by fetal sex during months 5 and 6 of pregnancy, and weeks 2–13 of lactation. Open circles represent mothers with female offspring (n=4), and closed circles indicate those with male offspring (n=4).

DISCUSSION

The broad patterns of change in fecal steroids over the peripartum period in this wild baboon population were the same as those previously reported in plasma, urine, or feces for captive baboons and other catarrhine primates [Bardi et al., 2001; Coe, 1990; Czekala et al., 1983; French et al., 2004; He et al., 2001; Heistermann et al., 1996; Hodgen et al., 1972; Maestripieri & Megna, 2000; Sholl et al., 1979], and for wild langurs [Ziegler et al., 2000]. The present analysis of peripartum steroid hormone concentrations in a wild nonhuman primate population is, to our knowledge, the first analysis to allow a comparison of experimental laboratory findings with results from unmanipulated wild primates of the same species at this critical life-history stage.

As predicted, primiparous females exhibited significantly higher estrogen concentrations than multiparous females during late pregnancy. These results are consistent with a preliminary study by Bahr [1995], who found that a captive primiparous gorilla had higher mean estrogen metabolite concentrations in the week prepartum than that observed in three of four pregnancies in multiparous gorillas. Our finding suggests that for primiparous baboons, high estrogen concentrations prior to birth may be important for organizing maternal responsiveness toward infants, and that high estrogen levels are not as important for multiparous females (see also Bridges [1975, 1996] for laboratory rats). The common practice of pooling data from primiparous females with those from multiparous females when measuring hormone concentrations and examining hormone–behavior interactions during the peripartum period will often confound interpretations of findings. In multiparous baboons, mothers carrying male fetuses have higher fT and fE concentrations than those carrying female fetuses during late pregnancy. The fT result is similar to the pattern reported for humans based on serum samples during the second half of pregnancy [Meulenberg & Hofman, 1991]. The fE result is similar to the pattern reported for urinary estrogen concentrations in female lemurs [Ostner et al., 2003; Shideler et al., 1983]. Higher estrogen levels in late pregnancy of lemur females carrying more male fetuses in their litters may reflect aromatization of androgens originating in the fetal testicles [Albrecht & Pepe, 1998; Ostner et al., 2003; Shideler et al., 1983]. Likewise, both fT and fE in the baboon mothers with males may also arise from steroids produced by the male fetus [Albrecht & Pepe, 1998].

For baboons, as for humans, differences in maternal steroid concentration based on fetal sex may vary across pregnancies, or be most clear only during late pregnancy and perhaps during specific developmental events for the fetus. Sampling at times of greatest difference in a primate species may permit at least a reasonable prenatal estimate of fetal gender in wild primate populations to be obtained, and thus may be useful in itself for studies of primate life-history patterns and population viability. In addition, the finding of differences associated with offspring sex raises the possibility that fetal sex differences contribute to endocrine and behavioral mechanisms of life-history variability, and to the social dynamics of the group.

In the Amboseli baboons, high maternal fT (but not other steroid concentrations) during the first postpartum months was predictive of subsequent infant death within the first year of life. This finding is paralleled by a body of literature on male parental care, which indicates that high testosterone appears to hinder care of young in some rodent and primate species in captivity (e.g., Mongolian gerbils [Clark et al., 1997], black-tufted-ear marmosets [Nunes et al., 2001], and cotton top tamarins [Ziegler et al., 1996]), as well as humans [Storey

et al., 2000]. Testosterone has not usually been measured in females. Our data did not support a potentially positive association between postpartum glucocorticoids and postpartum behavior in humans [cf., Fleming, 1990; Fleming et al., 1997b], or a negative association between glucocorticoids and postpartum outcomes in captive great apes [Bahr et al., 1998; Bardi et al., 2003]. Interestingly, in the one large-sample study of captive primates, Bardi et al. [2004] found that low prepartum and high postpartum glucocorticoids were associated with positive maternal behavior (testosterone was not measured in that study). Thus far, investigations of outcome have varied greatly in terms of the time periods and the range of behavioral, demographic, and endocrine measures examined, which may account for collective findings that are still few and difficult to interpret, and focus only on captive primates. Nonetheless, our results and those from other recent studies that examined individual profiles over time suggest the now-realizable potential of individual-based investigations of hormone–behavior associations that can be conducted noninvasively and are beginning to provide insights into the physiological mechanisms of life-history variability in natural primate populations.

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