Female hierarchy instability, male immigration and infanticide increase glucocorticoid levels in female chacma baboons

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Female baboons (*Papio hamadryas* spp.) must contend with myriad potential stressors on a daily basis. In a previous study on female chacma baboons, *Papio hamadryas ursinus*, living in the Okavango Delta of Botswana, increases in glucocorticoid (GC) concentrations were associated with female reproductive stage, male immigration and the threat of infanticide. Here, we extend this previous analysis to a larger data set with several additional potential stressors, including actual infanticide and instability in the female dominance hierarchy. A general linear mixed model showed that reproductive state, male immigration, infanticide, female rank instability and predation all had significant effects on GC levels. Lactating females' GC levels increased in response to the arrival of immigrant males and increased even further when infanticide occurred. In contrast, cycling and pregnant females' GC levels did not change. Females also showed elevated GCs in response to instability within their own dominance hierarchy, especially if their own ranks were at risk. Females' stress responses were frequent, but specific to events that threatened their own lives, the lives of their offspring, or their dominance ranks.

Dominance rank instability appears to be a major source of psychological stress for nonhuman primates (e.g. Stavisky et al. 2001; Barrett et al. 2002; Cavigelli et al. 2003; Mueller & Wrangham 2004; Sapolsky 2005). Although there is no simple correlation between dominance rank and glucocorticoid (GC) levels across taxa, meta-analyses have suggested that the degree to which dominants harass subordinates, the level of social support and the availability of outlets for aggression all influence the magnitude and direction of the relationship between GCs and rank (Abbott et al. 2003; Goymann & Wingfield 2004; Sapolsky 2005). In free-ranging groups of baboons (*Papio hamadryas* spp.), low-ranking males have higher basal GC levels than high-ranking males when the dominance hierarchy is stable (Sapolsky 1990; Bergman et al.

2005). During periods of rank instability, however, when the reproductive control enjoyed by high-ranking males is threatened, GC levels of high-ranking males are higher than those of low-ranking males (Sapolsky 1993, 2005; Bergman et al. 2005).

In contrast to males, subordinate females in such female-bonded species as baboons and macaques (*Macaca* spp.) show little evidence of rank-related stress (e.g. Stavisky et al. 2001; reviewed by Sapolsky 2005). Although stress and depression can be induced in low-ranking females under extremely abnormal captive conditions (e.g. Shively et al. 1997, 2005), under more natural conditions, low-ranking females receive comparatively little aggression and there is little if any reproductive suppression or skew (Silk 2002; Cheney et al. 2004). Moreover, because the female dominance hierarchy remains stable for years at a time (Samuels et al. 1987; Silk et al. 1999; Silk 2002), females' stress responses are by definition usually unaffected by female rank instability.

The immigration of an unfamiliar male is another well-documented source of psychological stress for baboons. An immigrant's rapid ascent in the male dominance

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hierarchy is accompanied by an abrupt increase in both males' and females' GC levels (Alberts et al. 1992; Sapolsky 1993). Among chacma baboons, *Papio hamadryas ursinus*, in the Okavango Delta of Botswana, the effect of an immigrant's rise to the alpha rank position is particularly pronounced (Beehner et al. 2005; Bergman et al. 2005), because such males often commit infanticide (Busse & Hamilton 1981; Collins et al. 1984; Tarara 1987; Palombit et al. 2000). Thus, a dominant immigrant poses a threat not just to male social stability but also to the survival of infants. Chacma males compete fiercely for alpha status, a position that ensures a virtual monopoly on mating activity (Bulger & Hamilton 1988; Bulger 1993). Alpha status, however, tends to be short-lived (Hamilton & Bulger 1990; Palombit et al. 2000; Cheney et al. 2004). Infanticide appears to be a sexually selected strategy that allows males to maximize their reproductive success during their short tenure in the alpha position (Palombit et al. 2000).

Beehner and colleagues (2005) found that the take-over of the alpha rank position by a potentially infanticidal immigrant male resulted in increased GC levels for lactating and pregnant, but not for cycling, female baboons. Even in the absence of any infanticidal attacks, females at risk of losing their offspring responded to the presence of a recent immigrant alpha male by mounting what appeared to be an anticipatory stress response. In contrast, when a natal male who was unlikely to commit infanticide achieved alpha status, there was no change in GC levels for any females.

As a counterstrategy to infanticide, lactating females often form 'friendships' with resident males, usually males with whom they mated during their conceptive cycle (Palombit et al. 1997, 2000; Palombit 1999). Male friends are more likely than other males to aid females under attack, especially when the aggressor is a potentially infanticidal male, and intervention by male friends reduces the likelihood of infant injuries or death (Palombit et al. 1997, 2000). Perhaps as a result, lactating females with male friends had lower GC levels during the immigrant male's take-over period than did lactating females without male friends (Beehner et al. 2005). In contrast, males with female friends tended to have higher GC levels after an immigrant take-over than did males without female friends (Bergman et al. 2005).

By necessity, Beehner et al.'s (2005) preliminary study dealt only with the threat of infanticide, because actual infanticide was not observed. They predicted that lactating females would show an even stronger stress response when actual infanticide occurred. Here we test this prediction. The current study included two periods of infanticidal attacks by immigrant males, allowing us to evaluate females' stress responses not only to the threat of infanticide but also to actual infanticide. In addition, this newer study augments the earlier one in several ways. First, it covers a much longer period of time (16 months versus 4) and includes considerably more behavioural and hormonal data. Second, although based on the same social group, seven (33%) of the females sampled in this study were not sampled in the previous study, and 11 of the 14 females previously sampled were in different reproductive states during the male immigration portion of this study.

Finally, and most unusually, during this newer study there were two incidents of rank upheavals in the female dominance hierarchy, providing us with a rare opportunity to examine the effects of female rank instability on female GC levels. We compare the stress responses of affected females to those of females whose ranks were unaffected, and examine the behavioural correlates of this response.

METHODS

Study Site and Subjects

The study was conducted over a 16-month period (May 2003–August 2004) in the Moremi Game Reserve, in the Okavango Delta of Botswana. The habitat consists of seasonal floodplains interspersed with slightly elevated wooded 'islands' (for a description, see Bulger & Hamilton 1987; Cheney et al. 2004). During the study, the group contained approximately 70 individuals, including an average of nine adult males and 22 adult females. The group has been observed since 1978 (almost daily since mid-1992), and all animals are fully habituated to human observers on foot. Maternal relatedness for all natal animals is known.

Like many other species of Old World monkeys, female baboons in this population form linear dominance hierarchies that usually remain stable over long periods (Silk et al. 1999; Bergman et al. 2003; Cheney et al. 2004). Females acquire ranks similar to their mothers', such that females from the same matriline typically occupy adjacent ranks (Silk et al. 1999). Females remain in their natal groups throughout their lives, whereas males usually emigrate to neighbouring groups at sexual maturity. Unlike females, adult males attain social rank through contest competition, and the male hierarchy is comparatively unstable (Bulger 1993; Kitchen et al. 2003).

Hormone Collection and Analysis

We collected 630 faecal samples for hormone analysis from 21 females over 16 months. All adult females (≥ 6 years of age at the beginning of the study) were sampled. On average, we collected one sample from each female every 2 weeks (mean $\pm$ SE = 13.99 $\pm$ 0.61 days) to obtain a mean $\pm$ SE of 30.00 $\pm$ 1.89 samples/female. No female was sampled twice before a faecal sample had been obtained from all other females. Hormones were extracted from faeces in the field using methods described by Beehner & Whitten (2004). All samples were assayed for GC metabolites using a corticosterone RIA kit (ICN Diagnostics Division) previously validated for use in baboons (Beehner & Whitten 2004). Samples were analysed in the laboratory of Patricia Whitten (Emory University). Mean $\pm$ SE interassay coefficients of variation were 12.16 $\pm$ 1.03% (high control, $N = 9$) and 8.82 $\pm$ 3.36% (low control, $N = 9$). The mean $\pm$ SE intra-assay coefficient of variation for a subset of 35 samples was 5.97 $\pm$ 6.81%. All samples were run in duplicate and mean concentrations are expressed in ng/g.

Methods of obtaining hormones from faeces generally must factor in a delay between hormone secretion (i.e.

circulating concentrations) and hormone excretion (i.e. faecal concentrations). In baboons, this lag time for GCs ranges from 24 to 72 h, with peak excretion occurring at 26 h (Wasser et al. 2000). Based on this estimate, we assumed a 24-h delay between social and demographic events and faecal samples reflecting hormonal changes resulting from these events.

Behavioural Data

Behavioural samples were obtained by methods identical to those described in Beehner et al. (2005). Briefly, we conducted 10-min focal samples on all females included in the hormone analysis throughout the study period. During each focal, we recorded all social interactions, including aggression and grooming. Aggression was defined to include vocal and visual threats, as well as physical attacks.

Statistical Analysis

We used general linear mixed models (GLMM) to assess the effects of seven categorical variables on GC levels. GC levels were normalized via log transformation. Because we sampled the same individuals repeatedly, we included individual identity as a random factor in the model with first-order autocorrelation as a covariance structure. We used restricted maximum likelihood methods for model estimation and Sattherwaite's F tests to gauge fixed effects. All GLMM analyses were performed in SPSS 12.0 (SPSS Inc., Chicago, Illinois, U.S.A.).

We used Akaike's information criterion (AIC) to choose the best model, starting with all main effects and interactions between each main effect and the random factor 'identity'. None of the interactions with identity were included in the final model. Additional exploratory analyses were conducted on reproductive state, male immigration, infanticide and female instability. In analyses comparing GC levels of all females, we used GLMMs with identity entered as a random factor. Because sample sizes for many analyses comparing subgroups of females and/or restricted time periods were often small, we used nonparametric statistics for these tests. Confidence intervals of effect sizes were calculated for Wilcoxon signed-ranks tests and Mann–Whitney U tests using R 2.1.0 (R Foundation for Statistical Computing, Vienna, Austria). All tests were two tailed, with adjusted P values listed in the text. We used Qvalue 1.0 (J. D. Storey, University of Washington, Seattle, Washington, U.S.A.) to correct for multiple testing (Storey 2002). Qvalue calculates a minimum false discovery rate (FDR), controlling the proportion of true null hypotheses that are rejected. Controlling for FDR among multiple tests is a more equitable compromise between type I and type II errors than is a Bonferroni correction. FDR is not as strict as traditional familywise corrections, so it retains more statistical power, which is especially important when sample sizes are small (Storey & Tibshirani 2001; Nakagawa 2004). We set the FDR at 0.05, and the π_0 value, obtained through the program's smoother function, was 0.4762. Readers should keep in mind that most of our exploratory analyses were necessarily conducted on small samples; therefore, power to detect small or medium-sized effects is low.

In this paper, we focus on four of the seven predictors described below: female reproductive state (predictor 3), male immigration (predictor 4), infanticide (predictor 5) and female dominance rank instability (predictor 6). We discuss the effects of predation (predictor 7) elsewhere (Engh et al. 2006). In the interest of clarity, however, we describe all seven predictors and their contributions to the model here.

(1) Age was divided into three classes, each representing approximately one-third of all samples: young (7–8 years), middle (9–14) and old (15–22), based on known birthdates.

(2) Dominance ranks were determined by the outcome of approach–retreat interactions (Silk et al. 1999). Females were classified as low- (relative rank 0.0–0.33), middle- (>0.33–0.66) or high- (>0.66–1.0) ranking, depending upon the proportion of females that they dominated at the beginning of each month.

(3) Female baboons' reproductive states are relatively simple to identify, because their perineal skins swell prominently during the oestrous cycle (Bielert & Busse 1983). We classified reproductive state as cycling (females in any stage of the oestrous cycle), pregnant (assigned post hoc from the birth of an infant as starting at the final detumescence of the perineal skin), lactating (the period following the birth of an infant until the resumption of cycling or the death of an infant) or other (the period after the death of an infant but before the resumption of cycling).

(4) Male immigration was a dichotomous variable with corresponding values for immigration (all samples collected during the 4 weeks after a new male joined the group) and no immigration (no males immigrated in the previous 4 weeks).

(5) If we witnessed an infanticidal attack or strongly suspected an adult male of attacking or killing an infant, all samples collected in the next 4 weeks were considered to be from an infanticidal period. Infanticide was strongly suspected when we observed infants with canine punctures, or when a previously healthy infant disappeared and its mother reacted strongly to a recent immigrant male's approaches. Mothers typically screamed and/or fled whenever the male approached for several days after the infant's disappearance (for further details see Cheney et al. 2004). There were six cases of confirmed or strongly suspected infanticide during the study period.

(6) The female dominance hierarchy was classified as either stable or unstable. Two periods of rank instability occurred during this study (described below). Samples collected during and in the 4 weeks following bouts of instability were coded as unstable.

(7) Samples were classified as positive for predation in the 4 weeks after one or more juveniles or adults was preyed upon or disappeared healthy (for a detailed analysis see Engh et al. 2006).

Seasonality was not included in the model because there were no seasonal effects on GC levels in either males or females (J. C. Beehner, unpublished data).

RESULTS

Factors Contributing to Elevated GCs

Our final model included reproductive state, male immigration, infanticide female rank instability and predation as significant predictors (Table 1). Neither age nor rank was included in the final model. The lack of a significant effect due to age or dominance rank suggests that females' GC levels were affected primarily by events rather than by their individual attributes. GC levels in samples collected during periods of relative calm (i.e. when the hierarchy was stable, no males had recently immigrated and no healthy troop members had disappeared) were similar to those found in the stable periods of Beehner et al. (2005).
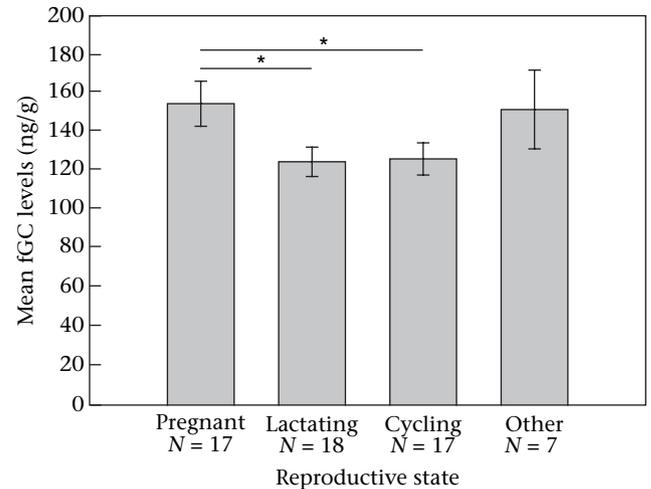
Reproductive State

Females in different reproductive states had significantly different mean monthly GC levels (GLMM: $F_{3,412.470} = 8.584$, $P = 0.004$; Fig. 1). Post hoc tests revealed that pregnant females had significantly higher GC concentrations than either cycling ($P = 0.004$) or lactating ($P = 0.004$) females. Females in the 'other' reproductive state had widely varying GC levels that did not differ significantly from pregnant ($P = 0.476$), lactating ($P = 0.159$) or cycling ($P = 0.169$) females' levels. These results are comparable to those obtained by Beehner et al. (2005) and Weingrill et al. (2004), who also documented the highest GC levels in pregnant females. Among mammals, maternal GC levels increase throughout pregnancy in response to ovarian hormones (Taylor 2001), so this result is not unexpected. On average, raw GC levels in pregnant females were approximately 20% higher than those of cycling and lactating females. These levels increased throughout pregnancy (GLMM: $F_{2,189.385} = 9.465$, $P = 0.004$), with GC levels of females in their third trimester more than 40% higher than those of females in their first trimester ($P = 0.004$).

Although consorting male baboons in this population experience a temporary elevation in GCs when consorting (Bergman et al. 2005), we did not find a similar pattern among females. Rather, females with sexual swellings who were in consort with males tended to have lower GC levels than swollen females not in consort, but the difference was not significant (GLMM: $F_{1,133.822} = 3.331$, $P = 0.075$). A pairwise analysis of females during consort

Table 1. Variables included in the final GLMM, with individual identity entered as a random variable

Parameter	Numerator df	Denominator df	F	P
Reproductive state	3	406.2	8.584	0.004
Male immigration	1	613.312	35.871	0.004
Infanticide	1	617.223	6.081	0.028
Female rank instability	1	618.608	6.743	0.021
Predation	1	609.798	6.966	0.021

Figure 1. Mean (+SE) faecal GC levels of females in different reproductive states. Significant differences are denoted by an asterisk.

and nonconsort across the same cycle revealed no differences in GC levels (Wilcoxon signed-ranks test: $T = -0.259$, $N = 16$, $P = 0.405$; CI: -37.59, 60.74 ng/g).

Male Immigration

Corroborating earlier results (Beehner et al. 2005), mean GC concentrations in females were significantly higher in the month following the immigration of one or more unfamiliar males than when no immigration occurred (Table 1). Females' GC concentrations were elevated regardless of whether or not one of the immigrant males took over the alpha position (GLMM: $F_{1,286.124} = 1.539$, $P = 0.185$). However, instability among immigrant males in the top of the male dominance hierarchy did appear to affect females' GC levels. Females' GC levels were significantly higher in months when there was instability in the top two positions in the male dominance hierarchy than in months when the top two positions were stable (GLMM: $F_{1,626.270} = 9.685$, $P = 0.008$), possibly because changes in rank among high-ranking males always involved at least one potentially infanticidal immigrant. This effect was restricted to instability at the top of the male dominance hierarchy; mean GC levels of females were no higher in months when there was instability in the lower portion of male dominance hierarchy than in stable months (GLMM: $F_{1,370.034} = 0.757$, $P = 0.269$).

During this study, there were only two short periods when we could assess the effects of male immigration on females in different reproductive states in the absence of other possible stressors. Each period was characterized by the arrival of a single immigrant male. Mean GC levels for cycling females were similar in the month before and after each male arrived (Wilcoxon signed-ranks test: $T = -0.700$, $N = 8$, $P = 0.290$; CI: -17.45, 46.28 ng/g). Although mean GC levels of pregnant females did rise, this difference was not significant ($T = -1.572$, $N = 13$, $P = 0.116$; CI: -10.37, 37.72 ng/g). In contrast, lactating females had significantly higher GC levels in the month

after male immigration than in the month before ($T = -2.201$, $N = 6$, $P = 0.044$; CI: 26.94, 78.22 ng/g; Fig. 2).

As in the previous study by Beehner et al. (2005), there were no changes in the mean rate that females in any reproductive state received aggression from adult males in the months after immigration compared to the months before (Wilcoxon signed-ranks tests: cycling: $T = -1.00$, $N = 5$, 4 ties, $P = 0.232$; CI: not applicable; lactating: $T = -1.095$, $N = 4$, $P = 0.219$; CI: -0.54, 1.62 acts/h; pregnant: $T = -0.813$, $N = 9$, 4 ties, $P = 0.275$; CI: -1.08, 3.50 acts/h). Similarly, rates of female–female grooming and female–female aggression did not change.
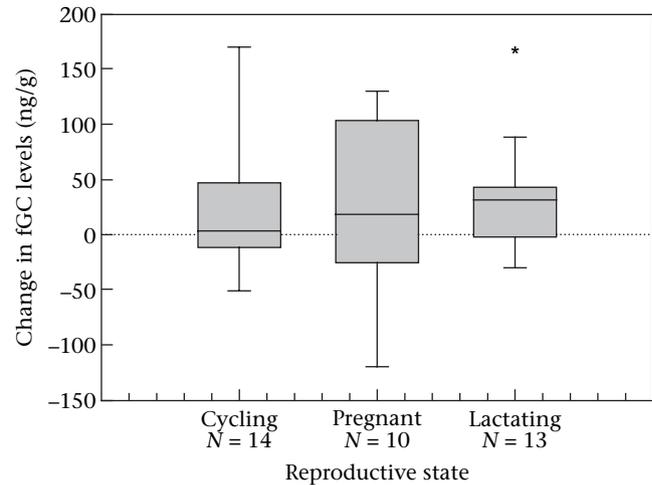
Infanticide

Two bouts of infanticidal attacks occurred during the study period, approximately 1 year apart. Females in all reproductive stages had higher GCs during the month after infanticide attempts were observed or strongly suspected than during periods without any infanticide (Table 1). To assess the effect of infanticide on females in different reproductive states while controlling for confounding variables, we conducted a pairwise comparison of females' mean GC levels during the infanticidal periods to their GC levels during the month before the infanticides began. Glucocorticoid concentrations for lactating females increased significantly during the infanticidal period (Wilcoxon signed-ranks test: $T = -2.132$, $N = 13$, $P = 0.045$; CI: 1.43, 54.20 ng/g), whereas levels of cycling and pregnant females remained unchanged (cycling: $T = -0.785$, $N = 14$, $P = 0.277$; CI: -15.68, 76.61 ng/g; pregnant: $T = -1.070$, $N = 10$, $P = 0.219$; CI: -51.66, 84.18 ng/g; Fig. 3).

Beehner et al. (2005) predicted that females with unweaned infants would have even higher GC levels during periods of actual infanticide than during periods when
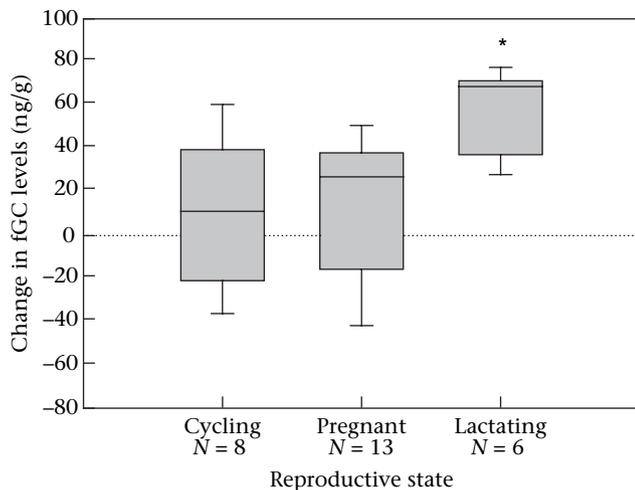
Figure 3. Change in GC levels of cycling, pregnant and lactating females during bouts of infanticidal attacks. Legend as in Fig. 2.
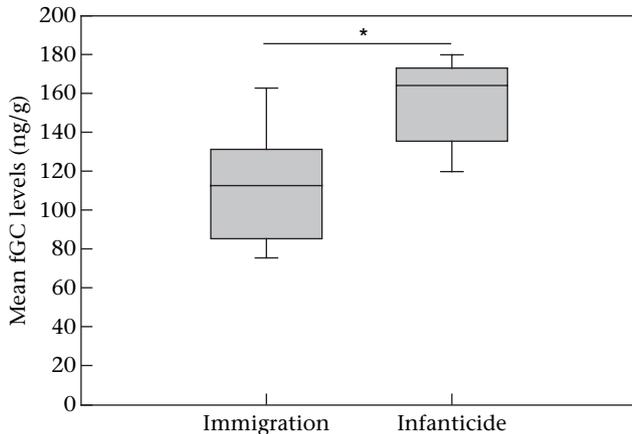
there was only the threat of infanticide due to the arrival of a high-ranking immigrant male. The second bout of infanticidal attacks proved a good opportunity to test this prediction, because it occurred during an otherwise uneventful period (i.e. when few animals disappeared as a result of predation).

Male SO immigrated during a period of male rank instability and rapidly ascended to the alpha position. Two months after entering the group, SO began attacking and killing infants. Mean GC levels of lactating females were significantly higher during the month when infanticides were occurring than during the previous month (Wilcoxon signed-ranks test: $T = -2.240$, $N = 8$, $P = 0.042$; CI: 17.28, 54.55 ng/g; Fig. 4).

Increases in females' GC levels were not the result of an increase in the overall amount of aggression received from males. For cycling females, the mean rate of aggression received from males tended to decrease during the infanticidal period compared to the month before (Wilcoxon signed-ranks test: $T = -2.040$, $N = 10$, $P = 0.051$; CI: -2.90, 0.00 acts/h). For lactating ($T = -0.944$, $N = 5$, $P = 0.246$; CI: -7.20, 2.54 acts/h) and pregnant females ($T = -0.314$, $N = 6$, $P = 0.389$; CI: -4.29, 12.00 acts/h), there was no change in the rate of male aggression. Rates of aggression received from females and rates of grooming were also unchanged.

The Effect of a Male Friend

In Beehner et al.'s (2005) study, lactating females with a male friend had lower GC levels after the arrival of a new immigrant male than did lactating females without a friend. We obtained similar results during infanticidal periods. Of the 13 females who had dependent offspring during the two infanticidal periods, five had a male friend. Females without a male friend showed a significant increase in GC levels during the infanticidal period (Wilcoxon signed-ranks test: $T = -2.38$, $N = 8$, $P = 0.032$; CI: 14.61, 95.73 ng/g), whereas GC levels in females with male friends did not change (Wilcoxon signed-ranks

Figure 2. Change in GC levels of cycling, pregnant and lactating females after the immigration of an unfamiliar male. Each box encompasses the 25th through 75th percentiles, with the median represented by an interior line. Whiskers denote 10th and 90th percentiles. An asterisk denotes a significant difference.

Figure 4. Mean GC levels of eight lactating females after an unfamiliar dominant male (SO) immigrated into the group and during a period of infanticidal attacks by SO. Legend as in Fig. 2.

test: $T = -0.135$, $N = 5$, $P = 0.432$; CI: -44.94, 72.32 ng/g; Fig. 5). On average, raw GC levels of females without a friend rose by 45%, whereas GC levels of females with a friend increased by 5%. GC levels were unaffected by female rank, because high-ranking females were not more likely to have a male friend during this period than were low-ranking females.

Female Rank Instability

Dominance ranks among female baboons typically remain stable for years at a time (Samuels et al. 1987; Silk et al. 1999; Silk 2002). With the occasional exception of orphaned juveniles, who sometimes attain ranks below or above those of their matriline (A. L. Engh, unpublished data), most females assume ranks similar to their mothers' and thereafter maintain the same relative rank throughout their adult lives. Before July 2003, there had been no changes in the relative ranks of the group's matrilines for at least 20 years. In that month, however, there was a brief attempt by a low-ranking matriline to overthrow
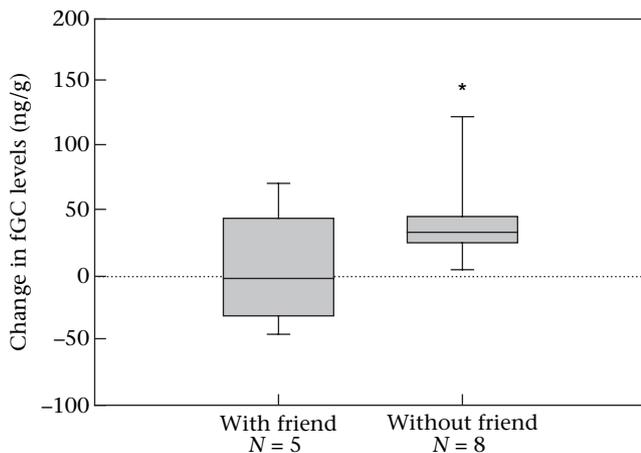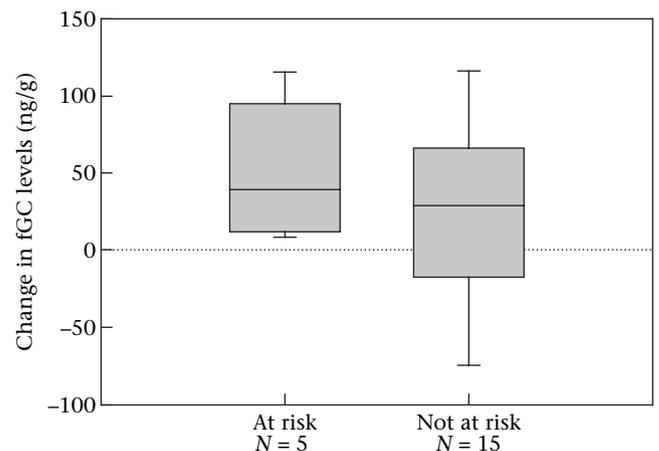
another. Several months later, three of six females from another, middle-ranking matriline were forced to the bottom of the hierarchy over a 3-month period. During these periods of instability, GC levels among females were significantly higher than during stable periods (Table 1).

First period of instability

During the first period of female rank instability, members of a low-ranking matriline attempted to overthrow the females in the matriline ranking immediately above their own. The lower-ranking matriline included an adult female and her adult daughter and sister; the higher-ranking matriline included an adult female and her two adult and juvenile daughters. The attempted overthrow was precipitated when members of the lower-ranking matriline and several adolescent females temporarily drove the adult female in the higher-ranking matriline from the group after she formed a sexual consortship with one of the group's adult males. Her daughters retaliated in her support, and for a week, members of both matrilines, as well as females from other matrilines, engaged in frequent, violent fights. The bulk of the fighting involved members of the two warring matrilines and a single, low-ranking adolescent female who consistently joined in support of the lower-ranking matriline. Females from both higher- and lower-ranking matrilines occasionally joined in the fighting, but their support shifted frequently. After a week of fighting, each matriline reverted to its original rank.

During the week of the upheaval attempt, there was a general increase in GC levels among all females compared with the week before the upheaval (Wilcoxon signed-ranks test: $T = -2.128$, $N = 20$, $P = 0.045$; CI: 7.26, 65.40 ng/g). This increase, however, was far more marked in females whose ranks were directly affected than in females whose ranks were not. GC levels for the five female members of the two warring matrilines tended to increase during the upheaval compared with the week before (Wilcoxon signed-ranks test: $T = -2.023$, $N = 5$, $P = 0.052$; CI: 8.64, 115.46 ng/g; Fig. 6), whereas GC levels

Figure 5. Change in GC levels during a period of infanticidal attacks for lactating females with and without male friends. Legend as in Fig. 2.

Figure 6. Change in GC levels during an attempted matrilineal overthrow. Females were classified according to whether their ranks were 'at risk' or 'not at risk' of changing. See text for more details. Legend as in Fig. 2.

of females in other matrilines did not (Wilcoxon signed-ranks test: $T = -1.806$, $N = 15$, $P = 0.169$; CI: -12.01, 69.85 ng/g).

Mean GC levels of females at risk of falling in rank ($\overline{X} \pm SE = 130.65 \pm 20.70$) were similar to those of the females in the challenging matriline (136.01 ± 34.15). Interestingly, mean GC levels of the unrelated females who participated in the fighting were not higher than those of the females who remained uninvolved (Mann–Whitney U: $U = 15.0$, $N_1 = 12$, $N_2 = 3$, $P = 0.355$; CI: -106.72, 72.32 ng/g).

Mean rates of female–female aggression during the week of the attempted overthrow ($\overline{X} \pm SE = 7.67 \pm 2.11$ incidents/h) were higher than the week before (4.32 ± 1.06 incidents/h; Wilcoxon signed-ranks test: $T = -1.824$, $N = 18$, 1 tie, $P = 0.075$; CI: -0.60, 9.00 acts/h). This tendency was due primarily to aggression directed towards the members of the two warring matrilines, who received aggression at twice the rate of members in other matrilines (Mann–Whitney U: $U = 12.5$, $N_1 = 13$, $N_2 = 5$, $P = 0.053$; CI: -18.21, 3.02 acts/h).

Second period of instability

The second period of rank instability occurred over a 3-month period and involved three members of a loosely bonded middle-ranking matriline made up of two groups of sisters, one aunt and one mother–daughter pair. The first member of this matriline to fall in rank was an adult female, Cat. After leaving the group to consort with the alpha male for several days, Cat was harassed and expelled from the group. After enduring attacks for a week, she was eventually allowed to rejoin the group, but the other females continued to threaten and attack her. None of Cat's sisters, aunts or nieces intervened on her behalf, and one of her sisters joined in the threats against her. The troop's lowest-ranking female, CP, a young adult with no surviving offspring or close relatives, took advantage of Cat's lack of social support. CP harassed Cat mercilessly. Initially, CP threatened Cat only when she was able to recruit high-ranking females to help her. However, within a week, CP and all other low-ranking females were able to dominate Cat individually, and Cat and her one-year-old daughter fell to the bottom of the hierarchy. During the next 3 months, one of Cat's sisters, her aunt, and their immature offspring were forced to the bottom of the hierarchy by lower-ranking females. None of these females defended themselves when threatened, and none of the other females intervened on their behalves. Another adult sister (the one who fought against Cat) and two adult nieces maintained their ranks.

In contrast to the previous period of rank instability, there was no general increase in GC levels among all females during this second prolonged period of instability compared with the months before (Wilcoxon signed-ranks test: $T = -0.414$, $N = 18$, $P = 0.357$; CI: -46.39, 36.45 ng/g). In particular, the six members of the two highest-ranking matrilines appeared to be unaffected. However, 10 of the 12 middle- and low-ranking females whose ranks were at risk of changing as a result of the instability tended to have increased GC levels (binomial test:

$P = 0.051$). GC levels for members of the matriline that fell in rank were no different from GC levels for members of matrilines that rose (Mann–Whitney U: $U = 14.0$, $N_1 = 7$, $N_2 = 5$, $P = 0.313$; CI: -48.47, 93.17 ng/g).

As in the previous rank upheaval attempt, overall rates of female–female aggression during the months of rank instability were significantly higher than during the months before (Wilcoxon: $T = -2.897$, $N = 18$, $P = 0.012$; CI: 5.26, 24.23 acts/h). This was again due primarily to high rates of aggression received by the three females who eventually fell in rank; these females received aggression at a rate five times higher than other females, a substantial but nonsignificant difference (Mann–Whitney U: $U = 8.0$, $N_1 = 15$, $N_2 = 3$, $P = 0.087$; CI: -100.26, 3.07 acts/h). They also initiated aggression at a significantly lower rate than did other females (Mann–Whitney U: $U = 4.5$, $N_1 = 15$, $N_2 = 3$, $P = 0.045$; CI: 0.18, 32.05 acts/h).

DISCUSSION

The body's immediate response to an acute stressful event is to elevate levels of circulating GCs, which serve to mobilize energy reserves and curtail nonessential metabolic processes, such as growth and reproduction. While adaptive over the short term, this 'flight or fight' response is physiologically costly when sustained over long periods (Sapolsky 2005). We found that predation, reproductive state, male immigration, infanticide and instability in the female dominance hierarchy were associated with significant increases in female GC levels in the following month, whereas dominance rank and age were not. Infanticidal attacks represent immediate survival risks for infants. Male immigration and female rank instability represent subtler psychological risks, but females nevertheless responded to these events with elevated GC levels.

Male Immigration and Infanticide

As in Beehner et al.'s (2005) study, female baboons responded to male immigration and infanticidal attacks when their offspring were at risk. Lactating females' GC levels increased in response to both immigration and infanticide. Pregnant females' levels also increased, although not significantly. In contrast, cycling females' GC levels did not change. The lack of a significant increase in the stress response of pregnant females in this study differs from the results obtained by Beehner et al. (2005), suggesting either that females may not always anticipate an infanticidal threat until they have vulnerable offspring, or that the low power of the test was insufficient to detect a small effect. Lactating females showed a greater increase in GC levels during periods of actual infanticide than during periods when an immigrant male only posed a threat of infanticide.

Beehner et al. (2005) found that females mounted a stress response to a take-over of the alpha rank position by an immigrant male, but not to one by a natal male. Thus, females responded to the threat of infanticide rather than to instability at the top of the male dominance hierarchy. Nearly all observed infanticidal attacks in this

population have been committed by a recent immigrant alpha male (Busse & Hamilton 1981; Collins et al. 1984; Tarara 1987; Palombit et al. 2000; Weingrill 2000). A single exception involved a recent immigrant who rose to alpha status soon after the attack (Palombit et al. 2000). Our results suggest that immigration, rather than the take-over of the alpha position, is the relevant stressor for females. Females' GC levels increased whenever a new male immigrated, regardless of whether or not he took over the alpha position. This response is likely to be adaptive, because most immigrants are young, fit males who are ascending in rank and represent an infanticidal threat.

Like Beehner et al. (2005), we found that lactating females with male friends had smaller GC increases during infanticidal periods than did lactating females without friends. In this population of baboons, females take a more active role than males in the formation and maintenance of friendships, and females with friends experience fewer attacks by potentially infanticidal males (Palombit et al. 1997, 2000). The comparatively lower stress levels manifested by lactating females with friends support the hypothesis that females recognize the risk posed by potentially infanticidal immigrants and actively attempt to compensate for this risk through the formation of friendships.

Female Dominance Rank and Rank Instability

In captivity, subordinate female macaques housed in close quarters with unfamiliar individuals experience depression, HPA axis disturbances, low levels of ovarian steroids and higher mortality rates (Shively et al. 2005). Similarly, under natural conditions, low-ranking male baboons show higher GC levels during periods of rank stability than do high-ranking males (Sapolsky 1990; Bergman et al. 2005). In contrast, neither we, Beehner et al. (2005), nor Weingrill et al. (2004) found any evidence of a relationship between rank and GC levels among free-ranging female baboons.

In comparison to both males and captive females living under extremely unnatural conditions, free-ranging female baboons lead relatively amiable and tranquil lives. In most species of Old World monkeys, including baboons and macaques, the correlation between female rank and reproductive success is only weakly positive (reviewed by Silk 2002; Cheney et al. 2004), and in this population of baboons, the competitive advantages enjoyed by high-ranking females are swamped by the effects of predation and infanticide (Cheney et al. 2004). As a result, high- and low-ranking females are equally likely to have close relatives available for grooming and other forms of social support (Silk et al. 2003, in press). Indeed, the close grooming relationships in which all females in this study participated may have mitigated any chronic stress associated with low rank, resulting in the lack of correlation between rank and GC levels. High-ranking female baboons are able to vent frustration at more targets than are low-ranking females, but the level of harassment they impose upon low-ranking females is moderate.

Upheavals in the female dominance hierarchy are extremely rare in baboons (Samuels et al. 1987; Silk 2002). It is perhaps not surprising, therefore, that the two periods of rank instability that occurred during this study appeared to be stressful, especially for those whose ranks were at risk of changing. During the first period, the GC levels of the five females belonging to the two battling matrilines tended to increase. Females belonging to other matrilines entered into the fray but did not experience elevated GCs. Similarly, during the second period of instability, females who were most at risk of changing ranks showed a strong tendency towards higher GCs, whereas high-ranking females whose ranks were unaffected by instability in the lower portion of the hierarchy, were unaffected. Our results are similar to those observed among spotted hyaenas, *Crocuta crocuta*, and among male baboons from the same social group. Spotted hyaenas are social carnivores that live in very baboon-like societies. Female hyaenas acquire their social ranks from their mothers, and rank relationships between matrilines remain stable for long periods (Holekamp & Smale 1991). Like our baboons, female hyaenas experienced increased GC levels during periods of acute social stress in which their ranks were presumably at risk of changing (Goymann et al. 2001). Similarly, during periods of instability among the top-ranking individuals, high-ranking male baboons experienced an increase in GC levels, an increase that was doubtless due in part to the loss of control and predictability associated with a potential fall in rank (Bergman et al. 2005; see also Sapolsky 1993, 2005).

During the two periods of instability, we observed no difference in the GC levels of females whose ranks might increase compared to those whose ranks might fall. During the first period of instability, all females who were at risk of changing ranks tended to experience increases in rates of aggression received. During the second period of instability, females whose ranks dropped received aggression at high rates, but females whose ranks rose did not. Because females who were ascending in rank experienced increased GC levels without a concurrent increase in aggression, it seems unlikely that the increase in GCs was related to aggression. Instead, our results suggest that instability in the female dominance hierarchy is stressful to females whose ranks are affected, independent of whether they actually receive more aggression or whether their rank is liable to rise or fall.

The lack of a significant correlation between rank and reproductive success in this population (Cheney et al. 2004) raises the question of why females would compete for rank at all. There are several possible explanations. First, high-ranking females in this group have higher fecundity than lower-ranking females, but this effect is offset by the effects of infanticide and predation, which are largely independent of rank (Cheney et al. 2004). Because rates of infanticide and predation vary substantially from year to year (Bulger & Hamilton 1987; Palombit et al. 2000; Cheney et al. 2004), however, it might always be worth fighting to attain or maintain high rank. Second, high-ranking females enjoy priority of access to preferred food resources, and their competitive advantage should be especially beneficial in times of food scarcity (Silk et al. 1999). Both periods of hierarchy instability took place during a moderate drought, and may have been the result of competition for food, although

there was no indication that any group members were suffering from malnutrition.

Similar brief bouts of instability in otherwise stable female hierarchies have been observed in wild baboons (Samuels et al. 1987) and in captive cercopithecine species (e.g. Ehardt & Bernstein 1986; Gygax et al. 1997). Changes in relative size or power of matrilines have been suggested as a possible cause of rank reversals (Silk & Boyd 1983; Cheney & Seyfarth 1990; Datta 1992), but neither matriline size nor power appeared to be obviously related to the events that we observed. The first bout of instability involved two equally sized matrilines, and the second consisted of attacks against members of the group's largest matriline. Neither of the matrilines targeted for reversal contained old or sick females, and neither had recently lost a female member. However, the large matriline in the second incident was composed primarily of sisters, aunts and nieces rather than mothers and daughters. Some of these individuals rarely groomed or interacted with one another, and they may therefore have been reluctant to defend each other. Two matrilineal overthrows observed by Gygax et al. (1997) were associated with changes in the male dominance hierarchy and thus the relative power of matrilines. In both instances, females from the same matriline as the new alpha male initiated fights and eventually reversed ranks with members of the highest-ranking matriline. None of the females who challenged higher-ranking females in our study were related to large adolescent or adult males residing in the troop, and males did not actively participate in the fights.

The instability that we observed might have been the result of reproductive competition. Samuels et al. (1987) observed that a period of female dominance rank instability in a troop of wild baboons was associated with reproductive status. At the onset of the unstable period, 63% of adult females were cycling, including the four females whose ranks fell. Similarly, in a study of captive macaques, a bout of severe, matriline-based aggression occurred as a large cohort of adolescent females reached menarche (Samuels & Hendrickson 1983). We suspect that the instability that we observed was also related to female reproductive competition. All targeted females were in oestrus when attacked, and at the onset of both unstable periods, an unusually large proportion of adult and adolescent females (>5 years old) were cycling or within months of menarche (54% and 68%, respectively). In both periods, attacks appeared to be initiated largely by adolescents and females without young offspring, although older and lactating females joined the fighting. Perhaps these females were attempting to restrict access to preferred mates so that their future offspring might benefit from the undivided attention of a male friend.

Conclusion

Under normal conditions, the stress response is an adaptive reaction to environmental, psychological and physiological challenges. When stress is chronic, however, its effects can be pathological (reviewed in Sapolsky et al. 2000; Sapolsky 2005; Shively et al. 2005). Among female yellow baboons, *P. h. cynocephalus*, cortisol levels increased and circulating lymphocyte counts decreased in the 2 weeks after an exceptionally aggressive male immigrated (Alberts et al. 1992). Although our corticosterone data cannot be directly compared to Alberts et al. (1992), it would not be surprising if the increased GC levels that we observed were associated with a similar compromise in immunocompetence, especially after the immigration of infanticidal males. Our study period was characterized by unusually high rates of female rank instability, male immigration and adult mortality, but even in more 'normal' years, baboons have to cope with immigration, instability, infanticide and predation on a regular basis. Females appeared to use several strategies to minimize their exposure to chronically elevated GCs. They formed friendships with males in an apparent attempt to mitigate the stressful effects of male immigration and infanticide, and they extended their social networks when a close relative died (Engh et al. 2006). Perhaps as a result, their stress responses were transient and specific, and their GCs tended to return to baseline levels within a few weeks following a stressful event. Females initiated stress responses when their own lives or the lives of their offspring were at risk, or when there was a potential for their own ranks to change. Mild levels of despotism, combined with stress-reducing relationships and a highly specific response to stressors may have protected females from many of the deleterious effects associated with chronic stress.

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