Social stressors and coping mechanisms in wild female baboons (*Papio hamadryas ursinus*)

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Abstract

We examined the social correlates of fecal glucocorticoid (GC) levels in wild female baboons during a period of social and demographic stability. Females' GC levels were not affected by individual attributes such as number of kin or dominance rank, nor could we detect any significant seasonal effects. Instead, GC levels were influenced by behavioral attributes that varied between individuals and within individuals across time. Pregnant and cycling females who received high rates of aggression had higher GC levels than others. In contrast, pregnant and cycling females who received grunts – vocal signals of benign intent – at high frequencies from dominant females had lower GC levels than females who received grunts at lower frequencies. Lactating females showed the opposite trend, apparently as a consequence of the high rate of grunting and intense, unsolicited attention that their infants received from others. All females experienced lower GC levels in months when they concentrated their grooming among a small number of partners than when their grooming was more evenly distributed among many partners. Although GC levels in female baboons are most strongly influenced by events that directly affect their reproductive success, subtle social factors associated with the loss of predictability and control also seem to exert an effect. Loss of control may be mitigated if a female is able to predict others' intentions – for example, if others grunt to her to signal their intentions – and if she is able to express some preference over the timing and identities of her grooming partners.
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Introduction

Although it is well established that traumatic events such as the loss of a close companion induce a stress response and elevated glucocorticoid (GC) levels in animals, much less is known about the effects of non-catastrophic, everyday social events on GC levels (Nelson, 2000; Romero, 2004; Reeder and Kramer, 2005). An emerging body of research suggests that a variety of factors, including level of social support the degree of control and predictability that individuals are able to exert over their daily lives, can all influence animals' stress responses independent of any specific event (Weiss, 1968; Abbott et al., 2003; Goymann and Wingfield, 2004; Sapolsky, 2004; Tama-shiro et al., 2005). For example, when their dominance hierarchy is stable, high-ranking male baboons (*Papio hamadryas* spp.) exhibit lower GC levels than low-ranking males. However, when a dominant immigrant male enters the group and threatens the male dominance hierarchy, high-ranking males – whose status is most at risk – exhibit higher GC levels than low-ranking males (Sapolsky, 1992, 1993, 2005; Sapolsky et al., 1997; Bergman et al., 2005). Humans' stress responses also appear to be influenced strongly by their perceptions of the degree of control and predictability that they have over their daily lives (e.g. Levine and Ursin, 1991; Marmot, 2004; Ray, 2004).

Individual differences in response to social events also affect GC levels. In their studies of male baboons in Kenya, Sapolsky and colleagues identified two types of "personalities" that influenced males' GC levels. Males with relatively low GC levels were able to distinguish between true stressors and minor

events, exert some control over the former, distinguish between good and bad outcomes, and release frustration by means of redirected aggression (Sapolsky and Ray, 1989; Ray and Sapolsky, 1992; Virgin and Sapolsky, 1997). In addition, low GC males demonstrated high levels of social affiliation—a coping mechanism known to reduce stress levels in a variety of species, including humans (Engh et al., 2006b; reviewed by Carter, 1998; Panksepp, 1998; Thorsteinsson and James, 1999; Bartz and Hollander, 2006).

Female baboons (*Papio hamadryas ursinus*) in the Okavango Delta of Botswana show elevated glucocorticoid levels in response to several ecological and social stressors that directly affect their reproductive success, including predation, male immigration, and the threat of infanticide (Cheney et al., 2004; Beehner et al., 2005; Engh et al., 2006a,b). In an apparent effort to cope with these stressors, lactating females who are at risk of infanticide attempt to form "friendships" with a long-term resident male (Beehner et al., 2005, Engh et al., 2006b), and females who have lost a close relative to predation temporarily expand their grooming network to include more partners (Engh et al., 2006a). At a proximate level, predation and the threat of infanticide are probably stressful because they are unpredictable and uncontrollable. The loss of a close relative also damages a female's social bonds, which in turn may affect her reproductive success (Silk et al., 2003b, 2006a,b). The behavioral responses that females adopt may function not only to strengthen and mend their social relationships but also serve as coping mechanisms to restore some predictability and control to their social interactions (Levine and Ursin, 1991; Ray, 2004).

Stress in Okavango female baboons is largely event driven. These events, however, may mask other, more subtle social factors that could also influence females' glucocorticoid levels. In this paper, we attempt to identify some of the social factors that may act to increase or decrease GC levels in free-ranging female baboons, independent of any traumatic event. Using data gathered over an 8-month period when there was no male immigration and relatively few deaths, we examine the correlation between females' GC levels and 20 demographic, ecological, and behavioral variables known or suspected to affect GC levels in primates and other animals. Some of these variables, like dominance rank and the number of close kin, represent relatively uncontrollable and static attributes of specific individuals. Other variables, including patterns of aggression, grooming, proximity, and vocalizations, describe more modifiable behaviors that may influence the degree of control and predictability that females are able to exert over their social interactions.

Dominance rank

Although dominant female baboons enjoy priority of access to scarce resources and have the opportunity to threaten more individuals than low-ranking females, previous studies of a number of Old World monkey species have found no consistent relation between female dominance rank and stress (Engh et al., 2006b; reviewed by Sapolsky, 2005). Because reproductive skew among female baboons is low, and because even very low-ranking females usually have close kin available as grooming partners, we predicted no significant correlation between female dominance rank and GC levels.

Number of close kin

Female baboons, like females in other Old World Monkey species, maintain strong, enduring bonds with close kin, who not only groom them at high rates but also support them in disputes, through either direct intervention or vocalizations (Silk et al., 1999, 2006a,b; Wittig et al., 2007b). The presence of kin is known to be associated with lowered stress in primates (Abbott et al., 2003), and previous research has shown that females in this population exhibit increased GC levels when they lose a close relative to predation (Engh et al., 2006a). As a result, we predicted that females with more close female relatives would exhibit generally lower GC levels than females with fewer relatives.

Aggression

We examined several patterns of aggressive behavior, including rate of aggression given and received, frequency of redirected aggression, and frequency of alliance support. The rate of aggression received reflects the intensity of social harassment, which is known to be stressful (Sapolsky, 1995; Wallner et al., 1999). In addition, there is some evidence that redirected aggression may help male baboons to divert anxiety and frustration (Virgin and Sapolsky, 1997); it has been shown to have stress-reducing effects in rats (Levine et al., 1989).

Close proximity

Closely related females are often, but not always, in close proximity to one another, which may act to increase affiliation and reduce stress. On the other hand, proximity may act as a social stressor for lower ranking females if it increases the likelihood of aggression from higher ranking individuals.

Grunting

Grunts are tonal, low amplitude vocal signals that are given at high rates by female baboons and function as signals of benign intent (Cheney et al., 1995; Silk et al., 1996; Rendall et al., 1999). They also function to reconcile opponents after aggression (Cheney and Seyfarth, 1997; Wittig et al., 2007a). Subordinate females appear to recognize that grunts are unlikely to be accompanied by aggression. If a dominant female grunts to a subordinate as she approaches her, the subordinate is significantly more likely to remain in close proximity than if the dominant female remains silent (Cheney et al., 1995). We therefore predicted that females who received grunts at a high frequency from higher ranking individuals would exhibit lower GC levels than females who received fewer grunts.

Grooming

Close bonds among female baboons, like those among females in other primate species, are manifested most obviously

in grooming interactions. We examined several measures of grooming given and received as well as grooming asymmetry and diversity. Female baboons typically concentrate their grooming among only a few individuals, who are usually close kin (Silk et al., 1999, 2006a,b). After their mother's death, females strengthen their grooming bonds with sisters; if females have few or no maternal kin available, they form bonds with paternal kin or non-kin (Silk et al., 2006a,b). And, as already mentioned, when they lose a close relative to predation females apparently attempt to compensate for this loss by seeking new grooming partners (Engh et al., 2006a). We predicted that females whose grooming network is stable should have a lower diversity of grooming partners than females whose network is unstable, and that females with a high diversity of grooming partners would exhibit higher GC levels than females with a low diversity of partners. A stable grooming network with a predictable, relatively small number of grooming partners is likely to serve as the primary coping mechanism for social stressors in female baboons.

In our analysis, we examine both between- and within-individual variation in GC levels and behavior. Tests of between-individual variation help to reveal differences in relatively static individual attributes, such as dominance rank and the number of close kin. They can also uncover the effects of individual differences in behavior, including, for example, variation in the diversity of grooming partners. Within-individual comparisons are more helpful in revealing which behavioral variables are associated with elevated or reduced GC levels. For example, comparisons of females' GC levels in months when they concentrate their grooming among a few partners as opposed to months when their grooming is distributed more evenly among a wide variety of individuals allow us to examine whether variation in females' GC levels are correlated with changes in the diversity of their grooming network.

Methods

Subjects and study site

The data described in this paper were gathered over an 8-month period from September 2004 through May 2005 as part of a long-term study of a troop of wild chacma baboons (*P. hamadryas ursinus*) in the Moremi Game Reserve in the Okavango Delta of Botswana. The group has been observed since 1978 and all animals are fully habituated to human observers on foot. At the time of this study, the group contained approximately 70 individuals, including nine adult males and 24 females over the age of 6 years, 8 females of $6 \geq 3$ years old, and 22–24 other juveniles and infants. The subjects of this study were 18 adult females (>6 years). Six adult females were not included because they had either not yet begun cycling at the start of the study period ($n=4$), were effectively menopausal ($n=1$), or died during the study period ($n=1$).

As in other species of Old World monkey, female baboons form stable, linear dominance hierarchies based on the direction of approach–retreat interactions and aggression. Females assume ranks similar to their mothers', so that matrilineal relatives typically occupy adjacent ranks (Silk et al., 1999, 2006a,b; Cheney et al., 2004). Females remain in their natal groups throughout their lives and maintain close bonds with close matrilineal kin, whereas males usually emigrate to neighboring groups at sexual maturity.

Behavioral sampling

We conducted 10-min focal animal sampling on females ≥3 years of age (the approximate age when females begin actively to groom other females)

during the 8-month period (range 650–710 min per female). During each focal sample, we recorded all of the subject's social and vocal interactions (including aggression, submission, grooming, proximity, etc.), as well as all approaches to within 2 m of the subject. At the end of each sample, we noted the identities of all individuals in close proximity (<2 m) to the subject and the subject's current activity (either eating, resting, moving, or grooming).

Aggressive behavior included physical attacks, chases, lunges, and vocal threats. Submissive behavior included retreats, turns away, crouches, and facial grimaces. Redirected aggression was scored when a female threatened a subordinate individual immediately after receiving aggression from a more dominant baboon. An individual was defined as receiving alliance support when a third party actively joined an ongoing conflict and threatened that individual's opponent (Wittig et al., 2007b).

Hormone collection and analysis

We extracted hormones from a total of 558 fecal samples during the 8-month period. Each individual was sampled once a week, and no female was sampled twice before a sample had been obtained from all other subjects. All samples were collected between 6:00am and 12:30pm (mean±SD of sample collection time=9:20 am±1:25 h), and GC levels did not vary with the hour of collection (mean±SD=136.8 ng/g [range=128.7–146.6]±65.6 [range=42.3–79.5]). Thus, confounding effects due to diurnal changes in GC levels (Van Cauter, 1990; Gust et al., 2000; Touma and Palme, 2005) were unlikely. Hormones were extracted from feces in the field using methods described by Beehner and Whitten (2004; see also Beehner et al., 2005) and analyzed in the laboratory of Dr. Patricia Whitten (Emory University). All samples were assayed for GC metabolites using a commercially available radioimmunoassay (RIA) kit.

In brief, steroid hormones were extracted from about 0.5 g of the fecal sample and immediately homogenized in 10 ml of methanol/acetone solution (4:1). After 4–10 h, the samples were separated from the fecal matrix using a 0.2-mm polytetrafluoroethylene (PTFE) filter followed by solid-phase extraction. Samples were stored on solid-phase extraction cartridges (Sep-Pak Plus C18 cartridges, Waters Associates, Milford, MA) at a subzero temperature until they were shipped to Emory University. After about 2 weeks, we recorded the dry weight of the residual fecal matter.

In the lab, steroids were slowly eluted from cartridges (3 ml 100% MeOH) and stored at −80 °C until the time of RIA. Samples were assayed to determine the concentration of fecal GC (fGC) using a modification of the ImmuChemä Corticosterone ^{125}I RIA kit (MP Biomedicals LLC, Orangeburg, NY, USA). The sensitivity of the assay, defined as the quantity of unlabeled steroid required to inhibit binding of the tracer by 2 S.D below the 0 ng/ml dose, was 0.7 ng/ml. The primary antibody reacted 100% with corticosterone, 0.34% with desoxycorticosterone, 0.1% with testosterone, and 0.05% with cortisol. All samples were run in duplicate and concentrations were expressed in ng/g (dry weight).

Immediately prior to RIA, aliquots of samples were evaporated under nitrogen and reconstituted in a working buffer. The working buffer was 0.1% gelatin phosphate-buffered saline (pH 7.4). ^{125}I tracer (50 µl) and antiserum (200 µl), diluted 1:3 in the working buffer, were added to 100 µl aliquots of the standards (diluted 1:3) to give concentrations of 20–1670 pg/ml), samples (diluted 1:20), and controls (diluted 1:3). Each was vortexed and incubated for 2 h at room temperature. After incubation, 500 µl of the second antibody (diluted 1:3) was added. The incubates were vortexed and incubated an additional 15 min at room temperature and centrifuged at $1500 \times g$ for 30 min at room temperature. Following decanting of the supernatant, the radioactivity of the precipitate was determined by 5-min counts in a gamma counter.

This method has been validated for use with baboons (Beehner and Whitten, 2004), has been used in several preceding studies of the same population (Beehner et al., 2005; Bergman et al., 2005; Engh et al., 2006a,b), and has been reviewed and approved by the Animal Car and Use Committee at the University of Pennsylvania (Protocol #19001). The intra-assay coefficients of variation (CV) averaged 3.4% over 40 sample duplicates ranging from 249 to 470 ng/ml. The inter-assay CVs for low and high serum controls from 14 assays were 14.7% and 12.1%, respectively.

For statistical purposes, we calculated the average GC level for each of the 18 females across 4-week blocks. The resulting data set was used in the model-building process and for post hoc analyses.

Statistical analysis

We extracted 3 demographic variables, 8 seasonal variables, and 16 behavioral variables from the focal samples. We subsequently had to eliminate 2 variables (redirected aggression and agonistic support received) that showed too little variance to justify further testing (<10% of values differed from zero), as well as 7 other variables that were highly correlated ($r > 0.7$; Tabachnick and Fidell, 2007) with at least one other variable that was entered into the model.

GLMM

We used general linear mixed models (GLMM) to assess the effects of the remaining 1 categorical variable and 17 continuous co-variables on GC levels. Because we sampled the same individuals repeatedly, we used a repeated measures model and included individual identity as a random factor in the model with a heterogenous co-variance structure. We log-transformed the dependent variable to achieve a normal distribution. We used restricted maximum likelihood methods for model estimates and Type III sums of squares for effect evaluation and calculated the Akaike's information criterion (AIC) to choose the best model. All GLMM analyses were performed in SPSS 15.0 (SPSS Inc., Chicago, IL, USA).

We created three models, one to test seasonal effects on GC levels, a second to test behavioral variables with pregnant female GC levels, and a third to test behavioral variables with non-pregnant female GC levels. We chose these three models for the following reasons.

First, several studies have indicated that GC levels can vary seasonally, depending, for example, on food availability, temperature, or seasonality in breeding (for reviews, see Romero, 2002; Weingrill et al., 2004; Touma and Palme, 2005). In order to reduce the number of variables, we first ran a model that included all seasonal variables in interaction with reproductive state (see below) and then included the final variables as predictors in the two behavioral models.

Second, it is well established that GC levels vary with reproductive state. Pregnancy is known to elevate GC levels significantly in female primates (French et al., 2004; Engh et al., 2006b; Beehner et al., 2006; Power and Schulkin, 2006). During the stable period, pregnant females' GC levels were on average >50% higher than cycling (paired t-test: $n = 9$, $t = -6.359$, mean difference -78.12, $P < 0.001$ with alpha=0.025 for Bonferroni correction) and lactating (independent sample t-test: $N_L = 6$, $N_P = 11$, $t = -3.865$, mean difference= -61.92, $P = 0.002$ with alpha=0.025) females', while cycling and lactating females' GC levels did not differ (independent sample t-test: $N_C = 8$, $N_L = 6$, $t = -1.931$, mean difference= -13.30, $P = 0.077$ with alpha=0.025). Because the elevated and highly variable GC levels in pregnant females had the potential to mask variation in GC levels due to more subtle individual or behavioral factors, we ran two separate GLMMs: one for pregnant and one for non-pregnant females. In the non-pregnant model, the behavioral variables were tested in interaction with reproductive state to determine if some behaviors had different effects on the GC levels of lactating and cycling females.

Because the model building of GLMMs is sensitive to empty values (Tabachnick and Fidell, 2007), we had to build the models based on data subsets using the maximum possible number of females while avoiding empty cells. We included samples from 10 pregnant females over a 4-month period from February 2005 to May 2005 in the first model and samples from 13 non-pregnant females over a 4-month period from October 2004 to January 2005 in the second model.

To begin building each model, we included the main effects, plus the interaction with reproductive state, of all variables and individual identity as a random factor. To ensure the integrity of the results from the GLMM, we eliminated as many variables as required to ensure that there were fewer variables than the number of subjects. In each model, the variables eliminated were those that explained the least variance. Thereafter, we used a stepwise backwards method to eliminate the variable that explained the least variance and then repeated the model building process again. This procedure was repeated until the elimination of another variable no longer increased the explanatory power of the model, as indicated by AIC score.

Post hoc tests

As GLMMs are sensitive to between-subject variation (random factor) as well as to within subject variation (repeated measures), we tested between-subject and within-subject effects post hoc. Post hoc testing included all available data on pregnant ($n = 11$) and non-pregnant ($n = 16$) females with samples for more than 2 months in a given reproductive state. We tested between-subject effects using Pearson correlations. When examining within-individual variation, we first determined the average value for a given pattern of behavior for each female and then compared below-average months with above-average months using a paired t-test. In each post hoc test, we used the maximum possible number of females. Outliers (values outside the 95% confidence interval) were excluded from the analysis.

Seasonal variables

Seasonal factors were analyzed using the variable *daylight hours*. *Daylight hours* measured the average difference between sunrise and sunset at the study site. *Daylight hours* were correlated with increased cortisol levels in female baboons living at a high latitude (Weingrill et al., 2004) and daylight hours were highly correlated with *maximum* and *minimum temperature* and *rainfall* at our study site. Activity budgets were calculated as the variation in the proportion of time spent feeding, moving, resting, and grooming. These data were gathered as point samples at the end of each 10-min focal sample.

The seasonal model included daylight hours and all four activity budget variables as main effects and each as an interaction with reproductive state.

Demographic and behavioral variables

We tested the effect of 1 categorical and 15 continuous variables on GC levels. The 16 predictors included the following:

1. *Reproductive state.* We classified three reproductive states: cycling (females in any stage of the estrous cycle), pregnant (assigned post hoc from the birth of an infant and starting at the final detumescence of the estrus cycle), and lactating (the period following birth until the resumption of cycling).

2. *Age.* Ageing in captive rhesus macaques, rats, and humans seems to blunt the stress response (Gust et al., 2000) and is associated with higher basal GC levels in wild baboons (Sapolsky and Altmann, 1991). The birth dates of all females were known (Cheney et al., 2004).

3. *Rank.* Each female's dominance rank was calculated monthly based on the direction of approach–retreat interactions (Silk et al., 1999). All females' ranks remained stable during the study period.

4. *Number of close relatives* was calculated as the number of females aged 3 years and older who were related to the subject through the maternal line by more than $r \geq 0.25$ (i.e. mothers, daughters, matrilineal sisters, grandmothers, granddaughters). Matrilineal relatedness was known for all females (Cheney et al., 2004).

5. Aggression was measured by two different variables. *Aggression received* was the rate of aggressive acts received per hour of observation time from any other individual. *Aggression given* was the rate of aggressive acts given per hour of observation time.

6. *Proportion of time in close proximity to others* was taken from scans at the end of each focal sample. *Close proximity* was calculated as # focal samples that ended when the subject was within 2 m of at least one other baboon over 3 years old/total # focal samples. (Three years of age was chosen to eliminate proximity resulting solely from the presence of young offspring.) Low values (approaching 0) indicated relatively asocial females; high values (approaching 1) indicated relatively social females.

7. Grunting behavior was measured from the perspective of both the vocalizer and the recipient. *Dominants' grunting behavior* described the proportion of approaches in which a female grunted when approaching a more subordinate female (# approaches toward subordinate females that included grunting/total # approaches toward subordinate females). *Grunting received from dominant* described the proportion of approaches in which a female was grunted to when

being approached by a more dominant female (# approaches by dominant females accompanied by grunts / total # approaches by dominant females).

8. Grooming was characterized by five measures. Grooming rates were minutes per hour spent grooming other females over 3 years old (*grooming given*) and minutes per hour being groomed by females over 3 years old (*grooming received*). Three grooming indices were also calculated:

   (a) *Shannon–Wiener Diversity Index* (SWDI) measured the diversity of a female's grooming partners. The SWDI was calculated using the formula from Wilson and Bossert (1971): $\text{SWDI} = -\sum_{i=1}^{s} p_i \log p_i$, with p_i being the proportion of total grooming with individual i, s the number of grooming partners, and log the natural logarithm. A low SWDI indicated that a subject concentrated the majority of her grooming among a few partners; a high value indicated that her grooming was more evenly distributed among all partners. During this study, the SWDI was highly correlated with total number of grooming partners (Pearson: $r = 0.783$, $P < 0.001$).

   (b) *Hinde Index for Grooming Partners* (HIGP) measured the proportion of partners whom a subject groomed relative to those who groomed the subject (derived from Hinde and Atkinson, 1970): $\text{HIGP} = \frac{P_A}{(P_A + P_B)}$, with P_A being partners that the subject groomed and P_B being partners that the subject was groomed by. A high HIGP indicated that the subject groomed more females than she was groomed by (active grooming); a low index indicated that she was groomed by more females than she groomed (passive grooming).

   (c) *Hinde Index for Grooming Time* (HIGT) described whether a subject received more grooming or gave more grooming: $\text{HIGT} = \frac{T_A}{(T_A + T_B)}$, with T_A being time that the subject groomed others and T_B being time that the subject was groomed by others. A high index indicated that she spent more time grooming others than being groomed by them; a low index indicated the opposite.

9. *Other friendly behaviors* included lipsmacking, touching noses or other body parts, and "ears back", an affiliative signal given to individuals who are out of reach.

Both pregnant and non-pregnant models included all 13 continuous variables plus *daylight hours*. However, the pregnant model investigated all of the variables as main effects, while in the non-pregnant model each variable was tested in interaction with the two reproductive states of cycling and lactating.

Results

Comparison of GC levels during stable and unstable periods

From the end of September 2004 through May 2005, the study group experienced few events known to increase GC levels in female baboons in this population (Beehner et al., 2005; Engh et al., 2006a,b). There were no challenges to the female dominance hierarchy, no upheavals in the alpha male position, no male immigration, no observed infanticidal attempts, no confirmed predation, and few disappearances. Two infants, two young juvenile males, and one 18-year-old low-ranking female with no close female relatives died during this time. The period therefore represented a time of relative stability. In contrast, during the 5 months following this stable period (June–October 2005), two males immigrated into the group and there were six changes in the alpha male position. In addition, one adult male, three adult females, and five infants died.

The period of relative stability was reflected in the GC levels of the 18 adult females (Fig. 1), especially when compared with the ensuing 5 months. From October 2004 through May 2005, females' GC levels were generally low and showed very little variance.

In contrast, mean values and variability increased dramatically during the subsequent, more eventful 5 months ($\text{GC}_{\text{stable}} \pm \text{SD} = 142 \pm 87.32$ ng/g; $\text{GC}_{\text{events}} \pm \text{SD} = 309 \pm 163.97$ ng/g). When comparing average GC levels and standard deviations between
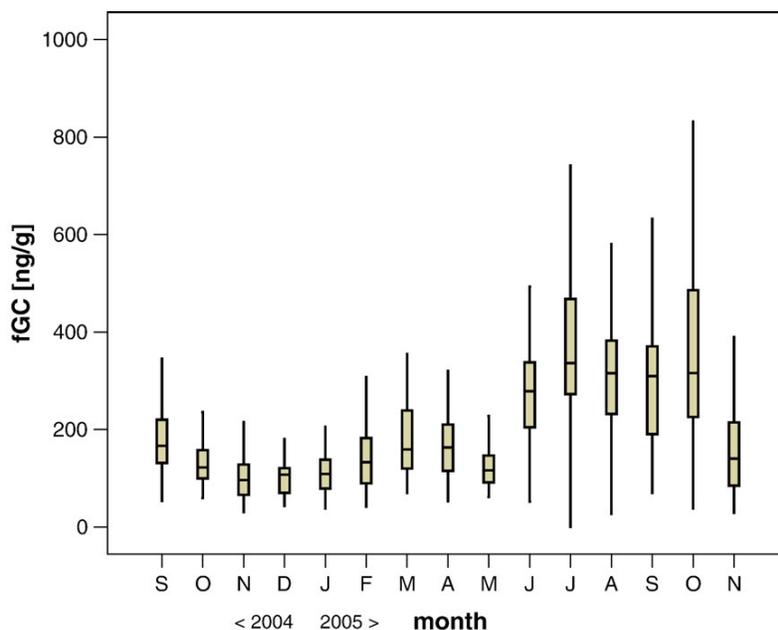

Fig. 1. The average monthly distribution of fecal glucocorticoid levels (fGC) in 18 adult females between September 2004 and November 2005. The period from 15 October 2004 to 30 May 2005 was a period of relative social stability, when there were no changes in the alpha male position, no male immigration, no observed infanticidal attempts, no confirmed predation, and few disappearances. Boxes show inter-quartile range and whiskers indicate 95% confidence intervals. Females' GC levels were significantly lower during the stable period than in the ensuing, less stable, 5 months.

Table 1
Females' mean fecal glucocorticoid (GC) levels during the stable and the event-driven period

Month	Stable/eventful	N	Mean GC [ng/g]	SD [ng/g]	Difference [a]
September 2004	E	17	177	43.2	>1 SD
October 2004	S	17	132	34.6	
November 2004	S	18	106	29.6	
December 2004	S	18	103	26.3	
January 2005	S	18	118	33.1	
February 2005	S	18	157	65.6	
March 2005	S	18	202	75.0	
April 2005	S	18	175	50.7	
May 2005	S	18	134	47.4	>2 SD
June 2005	E	18	281	85.3	
July 2005	E	17	382	110.8	
August 2005	E	17	339	81.8	
September 2005	E	16	297	64.4	
October 2005	E	15	380	99.4	>2 SD
November 2005	S	14	179	37.4	

[a] Difference between mean GC in two consecutive months (significant difference >standard deviations (SD); trend >1 standard deviation; no difference <one standard deviation indicated by empty cell).

consecutive months (Table 1), we found two significant changes (from May to June 2005 and from October to November 2005) and one trend (from September to October 2004). Thus, females' mean GC levels dropped at the beginning of the stable period and increased significantly during the transition from the stable to the event-driven period. All of the results described below were gathered during the 8 months of comparative stability.

Seasonal correlates of GC levels in female baboons

GLMM model

The final model included *daylight hours* and *daylight hours in interaction with reproductive state* (Table 2). The model suggests that females' GC levels decreased as daylight hours increased. The effect of *daylight hours*, however, disappeared and was replaced by an effect of *reproductive state* when both variables were entered as an interaction. Nonetheless, because both variables were significant they were included in the two behavioral models. No measure of activity budgets (time spent feeding, time spent moving, time spent resting, or time spent grooming) was included in the model, suggesting that females' GC levels were relatively unaffected by changes in metabolic needs, at least during this relatively short time period.

Post hoc tests

Between individual comparison

The majority of infants in the Okavango Delta are born between July and December, or at the end of the winter and beginning of summer (Cheney et al., 2004). As a result, in this study there were more pregnant females during winter months with shorter daylight hours than during summer months (Fig. 2). The percentage of females who were pregnant in each month was significantly correlated with average monthly GC levels across females (Pearson: $r=0.829$, $n=8$, $P=0.011$), whereas *daylight*

hours was not (Pearson: $r=-0.585$, $n=8$, $P=0.128$). A partial correlation with GC levels showed that the effect of *daylight hours* disappeared when the percentage of pregnant females was kept constant (Partial correlation: $r=-0.018$, $df=5$, $P=0.969$).

Within individual comparison

To further determine if *daylight hours* might be influencing females' GC levels, we examined the four females for whom reproductive state was constant across all eight stable months (all were lactating) and correlated each of their average monthly GC levels with daylight hours. None of the females' GC levels was affected by *daylight hours* (Pearson: female BL: $r=-0.479$, $n=8$, $P=0.230$; female CT: $r=-0.600$, $n=8$, $P=0.116$; female GI: $r=-0.232$, $n=8$, $P=0.581$; female SW: $r=-0.151$, $n=8$, $P=0.721$). In sum, there seems to be a seasonal effect on GC levels at this site that is explained by a seasonal influence on reproductive state; specifically, most females are pregnant during the months with the shortest daylight hours.

Social correlates of GC levels in female baboons

GLMM models

The final model for pregnant females included *rate of aggression received* and *grunting received from dominant* as significant predictors (Table 3). High rates of aggression were associated with higher GC levels, whereas high frequencies of grunting received were associated with lower GC levels. A low Shannon–Wiener Diversity Index for grooming (SWDI) was also associated with lower GC levels. Although this variable did not quite reach significance, we retained it in the model because the AIC score did not increase when it was taken out.

The final model for non-pregnant females included two indices of grooming asymmetry (Table 4). Specifically, cycling and lactating females who concentrated their grooming among a few individuals – and therefore had a low SWDI – had lower GC levels than those whose grooming was more equally distributed among partners. In addition, cycling females who were groomed by more partners than they groomed had higher GC levels than females who groomed more partners (HIGP).

Different behavioral variables therefore were significant in the pregnant and non-pregnant models. However, the SWDI for grooming was almost significant in the pregnant model, and the

Table 2
Predictors included in the final GLMM of seasonal effects, with individual identity entered as a random variable and month as a repeated measure ($n=18$, 8 months)

Predictor	Num.			Denom.			
Name	df	RS	Estimate	df	F	t	P
Daylight hours	1			55.7	18.6		<0.001
			−0.0603	57.7		−3.75	<0.001
Interaction: daylight hours × reproductive state	2			87.8	22.4		<0.001
		C	−0.0129	86.7		−6.36	<0.001
		L	−0.0099	114.7		−5.12	<0.001
		P	−[a]	−		−	−

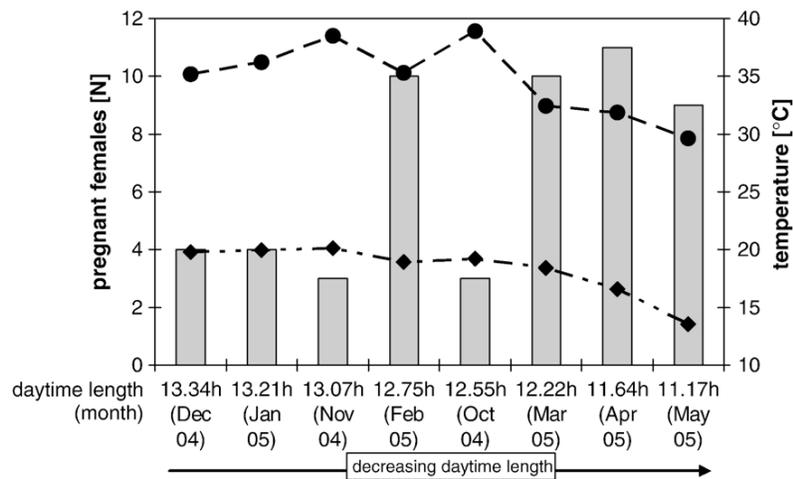Num.=numerator; Denom.=denominator; RS=reproductive state.
[a] Redundant values.

Fig. 2. The relationship between average day length, average maximum and minimum temperatures, and the number of pregnant females during each month. There were more pregnant females during months with shorter daylight hours.

two variables that were significant in the pregnant model (*rate of aggression received* and *grunting received from dominant*) were the last two variables to drop out of the model for non-pregnant females. We therefore decided to conduct post hoc tests on all three variables for females in each reproductive state. In particular, we wanted to conduct post hoc tests on *rate of aggression received* and *grunting received from dominant* for lactating and cycling females separately to ensure that the effects of one reproductive state did not mask behavioral effects in the other.

Finally, *daylight hours*, *age*, *rank*, and *number of close kin* were not included in either final model, suggesting that females' GC levels were relatively unaffected by seasonal factors and static individual attributes during this stable period.

Post hoc tests

Between-individual comparisons

The diversity of grooming partners (SWDI) was significantly correlated with GC levels in cycling females but not in pregnant or lactating females (cycling: $r=0.957$, $n=6$, $P=0.003$; lactating: $r=0.340$, $n=7$, $P=0.456$; pregnant: $r=0.103$, $n=11$, $P=0.762$). There was no significant correlation between the Hinde Index for Grooming Partners (HIGP) and GC levels for females in any reproductive state (cycling: $r=0.152$, $n=8$, $P=0.719$; lactating: $r=-0.629$, $n=7$, $P=0.131$; pregnant: $r=0.013$, $n=11$, $P=0.969$).

Cycling and pregnant females' GC levels were positively correlated with the rate of aggression they received (cycling: $r=0.971$, $n=7$, $P<0.001$; pregnant: $r=0.715$, $n=11$, $P=0.013$). There was no similar correlation for lactating females ($r=-0.270$, $n=7$, $P=0.558$), even though lactating and cycling females were threatened at generally higher rates than pregnant females.

Conversely, cycling and pregnant females' GC levels were negatively correlated with the frequency that dominant females grunted to them (cycling: $r=-0.892$, $n=6$, $P=0.017$, pregnant: $r=-0.727$, $n=9$, $P=0.026$). Lactating females' GC levels, however, showed a tendency in the opposite direction ($r=0.713$, $n=7$, $P=0.072$), despite the fact that they received grunts at a much higher rate.

Table 3

Predictors included in the final GLMM of pregnant females, with individual identity entered as a random variable and month as a repeated measure ($n=10$, 4 months)

Predictor	Num.		Denom.			
Name	df	Estimate	df	F	t	P
Rate of aggression received	1		24.1	5.5		0.027
		0.0642	24.1		2.35	0.027
Rate of grunting	1		19.7	14.1		0.001
		−0.9150	19.7		−3.76	0.001
SWDI	1		28.4	3.71		0.064
		0.072	28.4		1.93	0.064

Num.=numerator; Denom.=denominator; SWDI=Shannon–Wiener Diversity Index for grooming.

Table 4

Predictors included in the final GLMM of non-pregnant females, with individual identity entered as a random variable and month as a repeated measure ($n=14$, 4 months)

Predictor	Num.			Denom.			
Name	df	RS	Estimate	df	F	t	P
Interaction: HIGP × reproductive state	2			20.2	5.29		0.014
		C	−0.1940	17.5		−3.25	0.005
		L	−0.0327	23.7		−0.40	0.690
Interaction: SWDI × reproductive state	2			29.2	6.23		0.006
		C	0.1132	30.7		2.79	0.009
		L	0.0734	27.7		2.30	0.029

Num.=numerator; Denom.=denominator; RS=reproductive state; HIGP=Hinde Index for Grooming Partners; SWDI=Shannon–Wiener Diversity Index for grooming.
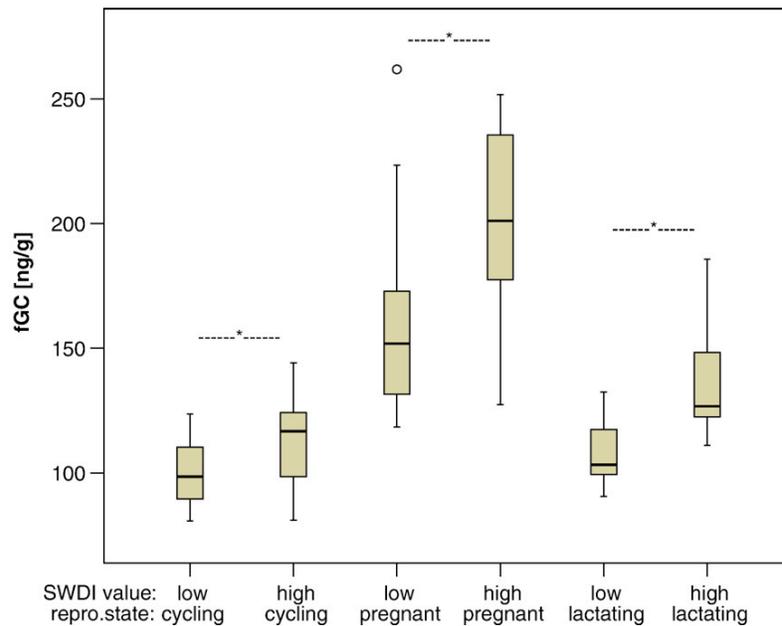
Fig. 3. Within-female comparison of fecal glucocorticoid levels (fGC) between months when they had a higher diversity of grooming partners (SWDI) than average and months when they had a lower diversity than average. Differences are presented separately for females in each reproductive state. Females had higher GC levels in months when they had a higher diversity of grooming partners. *$P < 0.05$. Boxes show inter-quartile range and whiskers indicate 95% confidence intervals.

Within-individual comparisons

We first determined each female's median value for the behavioral variables that were significant in the GLMM models and then compared each female's GC levels in above average months with her levels in below average months.

Post hoc analysis using the SWDI for grooming revealed that females in all reproductive states had lower GC levels in months when their grooming was concentrated on fewer individuals than average than when it was more equally distributed among partners (Fig. 3; paired *t*-test: cycling: lower than average = 100 ng/g, higher than average = 113 ng/g, *df* = 7, *t* = −2.543, *P* = 0.038; lactating: lower = 109 ng/g, higher = 138 ng/g, *df* = 6, *t* = −3.466, *P* = 0.013; pregnant: lower = 196 ng/g, higher = 199 ng/g, *df* = 9, *t* = −2.781, *P* = 0.021). There was no variation, however, in females' GC levels
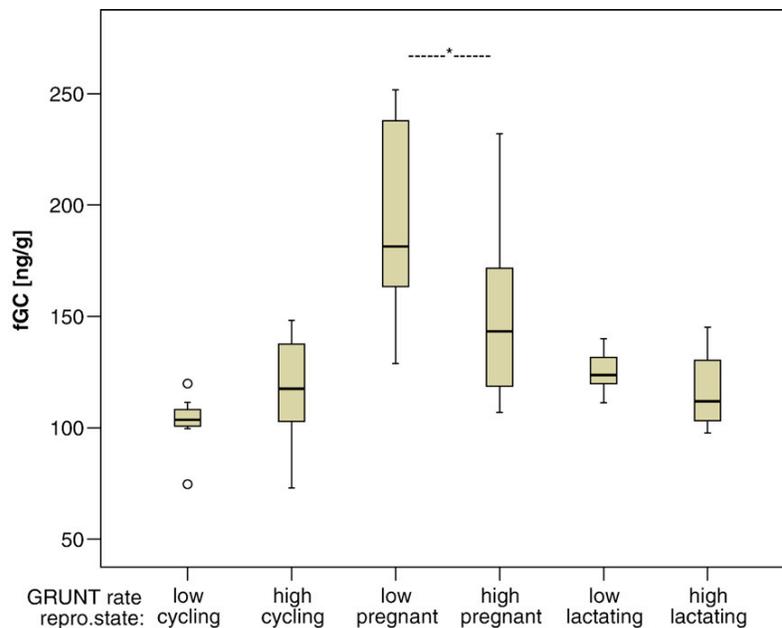

Fig. 4. Within-female comparison of fecal glucocorticoid levels (fGC) between months when they received grunts at a higher than average frequency from approaching dominant females and months when they received grunts at a lower than average frequency. Pregnant females had lower GC levels in months when they received grunts at a higher than average frequency. *$P < 0.05$. Boxes show inter-quartile range and whiskers indicate 95% confidence intervals.

between months when they groomed more partners than average or were groomed by more partners than average (HIGP) (paired *t*-test: cycling: lower=108 ng/g; higher=107 ng/g; *df*=7, *t*=0.076, *P*=0.942; lactating: lower=120 ng/g, higher=128 ng/g, *df*=6, *t*=−1.581, *P*=0.165; pregnant: lower=182 ng/g, higher=186 ng/g, *df*=10, *t*=−0.228, *P*=0.825).

Individual variation in females' SWDI might have occurred because females actively expanded their grooming networks in some months by seeking more grooming partners (high HIGP). Alternatively, an increased SWDI could also have occurred more passively, if females were being groomed by more partners (low HIGP). In fact, there was no consistent pattern between the diversity of a female's grooming network and her HIGP. Cycling females had a higher grooming diversity index in months when their HIGP was higher than average, indicating that they were grooming more partners (paired *t*-test: lower SWDI=0.335, higher SWDI=0.601, *df*=6, *t*=−5.541, *P*=0.001). In contrast, lactating females had a higher index in months when their HIGP was lower than average, indicating that they were being groomed by more partners (paired *t*-test: lower SWDI=0.309, higher SWDI=0.243, *df*=6, *t*=3.018, *P*=0.023). There was no relationship between pregnant females' SWDI and HIGP (paired *t*-test: lower SWDI=0.593, higher SWDI=0.587, *df*=10, *t*=−0.907, *P*=0.388).

We found no significant differences in GC levels for females in any reproductive state between months when they received lower than average rates of aggression and months when they received higher than average rates (paired *t*-test: cycling: lower=112 ng/g, higher=105 ng/g, *df*=7, *t*=0.585, *P*=0.577; lactating: lower=122 ng/g, higher=123 ng/g, *df*=6, *t*=−0.161, *P*=0.878; pregnant: lower=179 ng/g; higher=185 ng/g, *df*=10, *t*=−0.251, *P*=0.807).

Pregnant females had lower GC levels in months when they received grunts during a higher than average proportion of approaches than in months when they received grunts at a lower than average proportion (Fig. 4; paired *t*-test: *df*=7, *t*=2.556, *P*=0.038). There were no significant differences, however, for cycling or lactating females (paired *t*-test: cycling: *df*=6, *t*=−1.437, *P*=0.201; lactating: *df*=6, *t*=0.840, *P*=0.433).

Discussion

All females' GC levels were lower during this period of relative stability than during a subsequent more eventful period in which females' survival and reproductive success was directly threatened. Nonetheless, there was still some variation in females' GC levels, even after controlling for reproductive state. Although females had higher GC levels in months with shorter daylight hours, this effect appeared to be due to a seasonal influence on reproductive state because a higher proportion of females were pregnant during the southern latitude winter (Cheney et al., 2004). Furthermore, changes in activity budgets appeared to have little effect on females' GC levels. Instead, variation in females' GC levels was correlated with subtle behavioral attributes that varied between individuals and within individuals across time.

Our data do not allow us to draw definitive conclusions about the causal relation between GC levels and aggression, vocaliza-

tions, or the diversity of social networks. They do, however, support a number of the predictions described at the beginning of this paper, suggesting that some behaviors may have acted to increase GC levels, while others may have served as coping mechanisms to reduce them.

We could detect no over-riding effect of dominance rank on females' GC levels. This result is not surprising; even in captivity group-living female monkeys show little evidence of rank-related stress as long as they are not deprived of their social companions (e.g. Gust et al., 1994, 1996; Stavisky et al., 2001; Weingrill et al., 2004; Engh et al., 2006b; reviewed by Sapolsky, 2005). In most species of Old World monkeys, the correlation between female rank and reproductive success is only weakly positive (reviewed by Silk, 2002; Cheney et al., 2004), and subordinate females do not typically receive aggression at higher rates than more dominant females (Walters and Seyfarth, 1987; Abbott et al., 2003; unpublished data).

Perhaps more surprisingly, there was no relation between females' GC levels and matrilineal size. Female baboons tend to concentrate their grooming among a few close relatives (Silk et al., 1999, 2006a,b). However, when kin are not available females form stable grooming partnerships with non-relatives, which may mitigate any detrimental effects on stress or GC levels associated with the lack of close kin.

The primary factors influencing females' GC levels during this stable period appeared to be the control and predictability that they were able to exert over their social interactions. Pregnant and cycling females who received high rates of aggression from others had higher GC levels than females who received lower rates of aggression. In contrast, pregnant and cycling females who received grunts at a high frequency from approaching dominant females had lower GC levels than those who received grunts at a lower frequency. Furthermore, pregnant females had lower GC levels in months when they received grunts at a higher than average frequency. Grunts are signals of benign intent and are reliably associated with a low probability of aggression (Cheney et al., 1995; Silk et al., 1996). Moreover, playback experiments have demonstrated that grunts function to reconcile opponents following aggression (Cheney et al., 1995; Cheney and Seyfarth, 1997; Wittig et al., 2007a). Thus, grunts may mitigate the stress associated with aggression in part because they permit females to assess and predict the behavior of higher ranking animals.

Lactating females' GC levels, however, showed the opposite patterns. Although lactating females received aggression at higher rates than pregnant females, there was no correlation between lactating females' GC levels and the rate at which they were threatened. Moreover, in contrast to pregnant and cycling females, lactating females who received grunts from dominant females at a high frequency tended to have higher GC levels than those who received grunts at a lower frequency.

These results were probably a consequence of the intense attention that mothers with young infants receive from others. Female baboons with young infants are extremely attractive to other females, who groom them and attempt to handle their infants at high rates. These ostensibly friendly interactions are typically unsolicited (Seyfarth, 1976; Altmann, 1980; Silk et al., 2003a). Dominant females grunt to lactating females in over

90% of their approaches, compared to fewer than 25% of their approaches toward cycling and pregnant females (Cheney et al., 1995; Silk et al., 2003a). Moreover, over 50% of these approaches are followed by an attempt to handle the infant. Because females with young infants seldom initiate these interactions and often appear to be apprehensive about the attention they receive from more dominant females, the close association between grunts and infant handling may weaken the otherwise placatory effects of grunts as signals of benign intent.

Females in all three reproductive states had lower GC levels in months when they concentrated their grooming among a few preferred partners than in months when their grooming was more equally distributed among partners. However, there was no correlation between GC levels and absolute grooming time, nor with time spent grooming or being groomed for females in any reproductive state. These results suggest that females may experience increased GC levels when their grooming networks become less stable and discriminating. Working with the same group of baboons, Engh et al. (2006a) found a similar relationship between increased GC levels and an expanded grooming network. Females who lost a close relative to predation experienced a dramatic increase in GC levels, and they appeared to try to cope with this loss by expanding their grooming network, perhaps in an attempt to identify new grooming partners.

For cycling females, the correlation between higher GC levels and an increased grooming diversity index was also associated with higher rates of aggression received and lower frequencies of grunting by approaching dominant females. Cycling females' SWDI was higher in months when they groomed more individuals than they were groomed by. Cycling females may have actively attempted to extend their grooming network to appease aggressive females or to mitigate the effects of aggression in general.

In contrast to cycling females, lactating females' SWDI was higher in months when they were groomed by more partners than they groomed, indicating that the increase in their grooming diversity index was unsolicited. The lack of control that lactating females were able to exert over their grooming partners, in combination with the attention given to their infants, may have contributed to their increased GC levels. In support of this argument, Shutt et al. (2007) found that GC levels in pregnant female Barbary macaques (*Macaca sylvanus*) were lower in individuals who groomed others at higher rates than they were groomed, and who groomed more partners than they were groomed by.

Taken together, the results suggest a complex relationship between GC levels, active as opposed to passive grooming initiations, and grooming network size. Unstable, diffuse grooming networks are associated with higher GC levels. Although our results do not distinguish between the cause and effect of this association, we hypothesize that GC levels increase when the expansion of a female's grooming network is unsolicited and initiated by others. Lack of social support is strongly correlated with elevated stress hormones in a wide variety of primate species (Abbott et al., 2003), and it seems probable that a diffuse grooming network provides less social support than

one that is focused and selective. On the other hand, active expansion of a grooming network by females who have lost a preferred grooming partner or who are receiving increased aggression may function as a mechanism to reduce stress, at least in part because it may enable females to identify a new preferred grooming partner and to placate opponents. If this hypothesis is correct, increases in females' grooming diversity indices after the loss of a close companion should be temporary in nature and should decline again after they have established a new network of partners.

Numerous studies have shown that loss of control and damage to social bonds can increase stress in animals and humans, even in the absence of any specific event (see Introduction; see also Carter, 1998; Panksepp, 1998; Sapolsky, 2004; Marmot, 2004). Although GC levels in female baboons are most strongly influenced by events that directly affect their reproductive success, more subtle social factors associated with the loss of predictability and control also exert an effect. GC levels may be lower if a female is able to predict the intentions of others nearby – for example, if others grunt to her to signal their intent – and if she is able to express some preference over the timing and identities of her grooming partners. We might predict that, during unstable periods following a predator attack or the immigration of an infanticidal male, females who have a stable, focused grooming network should experience less stress. Furthermore, females should attempt to mitigate stress by increasing their grooming interactions with a few preferred partners.

Acknowledgments

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