The effect of new alpha males on female stress in free-ranging baboons

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In chacma baboons, *Papio hamadryas ursinus*, young adult males often rise to the top of the dominance hierarchy shortly after immigrating to a new group. Such events are potentially disruptive for pregnant and lactating females because high-ranking immigrant males often commit infanticide. In this preliminary study, we assessed the effects of upheavals in the male hierarchy on the physiology of 18 females in a baboon group living in the Moremi Game Reserve, Botswana. We collected behavioural and hormonal data to examine the effects of two separate events, a natal male take-over and an immigrant male take-over, on female faecal glucocorticoids (fGC). While few females had elevated fGC concentrations in response to the natal male take-over, following the immigrant male take-over there was a significant rise in fGCs, but only among lactating and pregnant females. Analysis of behavioural data indicated that elevated fGC concentrations were unrelated to male aggression towards females, female–female aggression, or rates of female–female grooming. Furthermore, lactating females with a male 'friend' during the immigrant male take-over period had a less marked increase in fGCs and lower fGC concentrations overall than females without a male friend. Taken together, these results suggest that male social instability itself does not necessarily elicit a stress response from females. Rather, it is the specific male that rises to the alpha position that prompts a stress response, and only from the females at risk for infanticide. Finally, females with a male friend may perceive themselves to be at a reduced risk of infanticide.

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Life in a social group subjects individuals to a variety of physical stressors, including agonistic encounters, running from a rival, or producing energetically costly displays. The stress response is an adaptive reaction to such challenges because it mobilizes energy reserves needed to cope with these immediate demands. In vertebrates, the stress response sets into motion a cascade of events that ultimately results in glucocorticoid (GC) secretion by the adrenal cortex (Sapolsky 2002). Glucocorticoids increase the availability of glucose in the bloodstream by promoting glucose production and curtailing glucose uptake and storage (Nelson 2000). Although chronic activation of the stress response can lead to pathology, the anabolic processes that accompany short-term challenges are an essential and adaptive response.

While the stress response is generally triggered by physical challenges, in some cases the cause of stress can be psychological. Low-ranking individuals, for example, may show elevated GC levels not because they receive more aggression but because they anticipate doing so. The widespread evidence of psychological stressors in human society (e.g. Sapolsky 2002) raises the possibility that group-living animals may show a stress response not just to events involving themselves but also to events that have the potential to do so.

In baboon societies (*Papio* spp.), the immigration of an adult male into a new group can be a potential source of psychological stress for both males and females. This is especially true when the immigrant male challenges high-ranking resident males, creating instability in the male dominance hierarchy. The disruption caused by the immigration of a male who quickly rises to the most dominant, or alpha, position may be reflected by a sharp elevation of GCs in both males and females (Alberts et al. 1992; Sapolsky 1993a; Palombit et al. 2000).

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Among chacma baboons, *Papio hamadryas ursinus*, in the Okavango Delta of Botswana, the arrival of a high-ranking immigrant male appears to have a particularly disruptive impact on pregnant and lactating females, because such males often commit infanticide (Busse & Hamilton 1981; Collins et al. 1984; Bulger & Hamilton 1987; Tarara 1987; Palombit et al. 2000). In the Okavango baboons, male mating activity is strongly correlated with dominance rank, and the alpha male monopolizes most mating (Bulger 1993). However, turnover in the alpha rank position is also high, and a male is usually able to maintain alpha status for only approximately 6 months (Hamilton & Bulger 1990; Palombit et al. 2000). Infanticide appears to be a sexually selected strategy that accelerates the return to fertility in lactating females, permitting the infanticidal male to mate with as many females as possible during his short tenure in the alpha position (see reviews in Hrdy 1974; Ebensperger 1998). In the population of chacma baboons discussed in this paper, infanticide is the single most important cause of infant mortality (Cheney et al. 2004).

Perhaps in response to the threat of infanticide, lactating females often compete to form close, affiliative relationships, or 'friendships', with specific adult males (Busse 1984; Palombit et al. 1997, 2000, 2001; Palombit 1999; Weingrill 2000). Observational and experimental data indicate that male friends are more likely than other males to aid females under attack, especially when the aggressor is a potentially infanticidal alpha male (Palombit et al. 1997, 2000). Intervention by male friends considerably reduces the likelihood of infant injuries or deaths (Palombit et al. 2000).

In populations where the risk of infanticide is high, an early termination of investment in potentially 'doomed' offspring might be adaptive because the loss of a pregnancy would reduce overall reproductive fitness considerably less than the loss of an infant (Ebensperger 1998). While this behavioural phenomenon has been demonstrated in many laboratory species (particularly rodents), field studies on wild populations are less conclusive (Ebensperger 1998; de la Maza et al. 1999; King & Allaine 2002; Mahady & Wolff 2002). Following the immigration of a highly aggressive male into one group of yellow baboons in Kenya, Pereira (1983) reported an increase in serious injuries among both adult males and females, an elevated rate of fetal loss, and one infant death. In this same population, another male immigration was associated with significantly higher rates of aggression, marked elevations in GCs, and a similar increase in fetal loss among group females (Alberts et al. 1992). These observations suggest that the arrival of an unfamiliar and aggressive male may result in early termination of pregnancy in baboons. While slightly elevated GCs are necessary to maintain a pregnancy, chronically elevated GCs exert an inhibitory effect on the female reproductive system (Bronson 1989).

In this preliminary study, we assessed the effects of new alpha males on the physiology of 18 females in a group of chacma baboons living in the Moremi Game Reserve, Botswana. We used both behavioural and hormonal data to examine the degree to which upheavals in the alpha rank position influenced the levels of stress-sensitive GC metabolites excreted in faeces (fGC). First, we compare fGC levels during periods of male social instability with those during periods when the alpha position was stable. As we were particularly interested in whether females respond to instability in general or to the threat of infanticide in particular, we separated females into reproductive categories based on risk of reproductive failure: pregnant and lactating females (high risk) and cycling females (low risk).

Second, we compared two turnovers in the alpha position that differed in infanticidal threat. The first occurred when a natal male rose to the alpha position. Although it is unclear why natal males who achieve high rank should refrain from committing infanticide, behavioural observations and demographic data gathered since 1992 suggest that such males rarely, if ever, attack infants (D. L. Cheney & R. M. Seyfarth, unpublished data). Moreover, although lactating females with infants flee from high-ranking immigrant males, they do not avoid similarly ranked natal males. The second change occurred when two unfamiliar immigrant males entered the group and usurped the natal male from the alpha position. As already mentioned, long-term data indicate that high-ranking immigrant males often attempt to commit infanticide, causing a high proportion of infant mortality (Palombit et al. 2000; Cheney et al. 2004). The comparison between the natal male and the immigrant male take-over period allows us to separate the roles of male rank instability from infanticidal threat. We hypothesized that, if females respond to any evidence of instability in the male dominance hierarchy, fGC levels in all females should rise during both rank changes. By contrast, if females respond specifically to the threat of infanticide, we predicted that fGC levels would show little change during the first male take-over but rise significantly during the second, and that this rise would be particularly evident in pregnant and lactating females.

We also examined overall rates of aggression and grooming across time periods to determine whether changes in females' stress response were correlated with behavioural changes in the group.

Finally, using a small sample of data we examined whether the formation of a friendship with a resident adult male dampened changes in females' stress responses.

METHODS

Study Group

Research was conducted in the Moremi Game Reserve in the Okavango Delta of Botswana (23°02'E, 19°31'S). Grasslands in the delta flood annually (usually between June and October), leaving elevated 'islands' edged with woodland (Hamilton et al. 1976; Bulger & Hamilton 1987; Ross 1987; Ellery et al. 1993; Cheney et al. 2004). Islands range in size from less than 1 ha to more than several hundred hectares. During floods, baboons ford the submerged plains and move between islands throughout an approximately 5-km^2 range.

The study group, C, has been observed since 1978 (e.g. Bulger & Hamilton 1987). Since mid-1992, the group has been under continuous observation on an almost daily basis. The ages and matrilineal relatedness of all natal animals are known, as are the origins and destinations of many immigrant males. The group is fully habituated to humans on foot. During the course of this study, the group contained 82–91 individuals, including 9–11 adult males (>8.5 years), 29–31 adult (>6 years) females, and their immature offspring.

As in many other species of Old World monkeys, female baboons remain in their natal group throughout their lives, maintaining close bonds with their matrilineal kin. Females can be ranked in a linear dominance hierarchy that is stable over time, accurately predicts the outcome of competitive interactions, and has matrilineal kin occupying adjacent ranks (Hausfater et al. 1982; Samuels et al. 1987; Silk et al. 1999). Although male baboons usually emigrate to neighbouring groups at around 8–10 years of age, some males occasionally remain in their natal groups and achieve high dominance status (Hamilton & Bulger 1990; Kitchen et al. 2003). Dominance relationships among males are considerably less stable than those among females and are influenced primarily by age, size and fighting ability (Hamilton & Bulger 1990; Bulger 1993; Kitchen et al. 2003). Due to the high degree of sexual dimorphism, even the lowest-ranking adult male is dominant to the highest-ranking female.

Here we use the term 'take-over' to indicate a change in the alpha rank position in the male dominance hierarchy. Unlike some other monkey species where former alpha males are sometimes (or always) ousted from the group (Struhsaker & Leland 1987; Pope 1990; Borries 1997), in baboon groups, the former alpha male generally continues to reside in the group.

Due to budgetary constraints and the preliminary nature of this investigation, we collected hormones from only 18 of the 31 adult females in the group. The females we selected for hormone sampling included representatives from three reproductive categories (cycling, pregnant, lactating), from different rank positions (high, middle and low) and from different age groups (old, prime and young adult, see definitions below). Faecal samples were collected only during the four periods described below. Our goal was to obtain samples from females during periods of male social stability and to compare these with periods of male instability. For this reason, we collected samples from relatively short, but discretely defined periods that could be categorized as stable or unstable.

(1) Stable period (before): 18 February–16 March. This was the final month of an unusually stable period when the same male had occupied the alpha rank position for almost 2 years. We call this period 'stable' although this refers to the stability of the alpha position, and not necessarily to the ranks of the other males. In fact, a natal male was rapidly rising in rank during this time.

(2) Natal male take-over: 17 March–16 April. This period began when the rising natal male from the previous period achieved the alpha rank position.

(3) Immigrant male take-over: 17 April–16 May. This period began with the arrival of two immigrant males, both of whom rose immediately to the first and second rank positions, usurping the natal male, who fell to the third rank position. The first and second rank positions remained ambiguous during this period, and the two immigrant males vied for the alpha rank position until one of them emigrated in mid-July.

(4) Stable period (after): 26 August–17 October. The remaining immigrant male assumed the alpha position following the emigration of the other male. We allowed the male hierarchy to stabilize before resuming female hormone collection. This period, therefore, represents a stable period after the social upheaval in the male dominance hierarchy had subsided.

Females were classified as either cycling, pregnant, or lactating. Cycling females included females in any stage of the oestrous cycle (menstruating, flat, or 'swollen', based on the condition of the sexual skin). Pregnancy was assigned post hoc following the birth of an infant from the last detumescence of the sexual skin (d-day) to the day before birth. No incidents of fetal loss were observed during this study. Lactation was assigned to all females following the birth of an infant up until the resumption of cycling. Pregnant and lactating females were grouped for most analyses. Of the 18 females from whom hormone data were obtained, 13 were pregnant or lactating and five were cycling across the four periods. Four females gave birth (changing from pregnant to lactating) but none of the pregnant and lactating females resumed cycling or conceived during the study period. One lactating female (SL) was added after the second observation period.

Male and female dominance ranks were determined through daily observations of approach–retreat interactions (supplants), using both focal animal and ad libitum sampling (Altmann 1974). Male and female dominance hierarchies were recalculated monthly. All ranks were expressed as the proportion of individuals dominated, allowing us to compare ranks across periods when the number of adult females in a given reproductive category changed. Female ranks were completely stable and strictly linear during the study period, while male ranks were much more dynamic (Bulger 1993; Kitchen et al. 2003). For each time period, dominance ranks were split into thirds, resulting in three rank categories (high, middle and low).

Female ages were based on known birthdates for all target females. Adult females ranged in age from 6 to 18 years. We grouped females into age categories by dividing the age range into 'young adult' (6–9 years), 'prime adult' (10–14 years) and 'old adult' (15–18 years).

Hormone Collection and Analysis

Although a higher percentage of GC metabolites are excreted in urine (for baboons, urine: 85–87%, faeces: 13–15%, Wasser et al. 2000), for a terrestrial primate that lives in a sandy environment it is generally easier and more reliable to collect faecal samples. We collected a total of 260 faecal samples for hormone analysis from 18 females

over the four periods. On average, we collected 3.5 samples per female per time period (range 1–7 samples per female per time period). All samples were collected during periods of low or no precipitation, at the start and end of the seasonal flood (Fig. 1). As a result, there were probably only minimal seasonal effects on hormonal concentrations. Because of our restricted sampling schedule, we were unable to examine the degree to which seasonal variation might influence GC concentrations.

Hormones were extracted from faeces in the field using methods described by Beehner & Whitten (2004). In brief, we collected approximately 0.5 g of faeces from known individuals during morning hours only and immediately homogenized the faeces in 10 ml of methanol:acetone (4:1). Later the same day, samples were separated from the faecal matrix using a 0.2-µm polytetrafluoroethylene (PTFE) filter followed by solid-phase extraction. Samples were stored on solid-phase extraction cartridges (Sep-Pak Plus C18 cartridges, Waters Associates, Milford, Massachusetts, U.S.A.) at a subzero temperature ($-10°C$) until transported to Emory University for analysis. At Emory University, steroids were eluted from cartridges with 3 ml of methanol and subsequently frozen ($-80°C$) until the time of radioimmunoassay (RIA). Immediately prior to RIA, aliquots of samples were evaporated under nitrogen and reconstituted 1:1 in working buffer (phosphosaline gelatin). All samples were assayed for GC metabolites using a corticosterone RIA kit (ICN Diagnostics Division, Costa Mesa, California, U.S.A.) previously validated for use in baboons (Beehner & Whitten 2004). Interassay coefficients of variation were $9.81 \pm 3.29\%$ (high control, $N = 14$) and $15.37 \pm 1.99\%$ (low control, $N = 14$). The intra-assay coefficient of variation was $8.98 \pm 5.19\%$
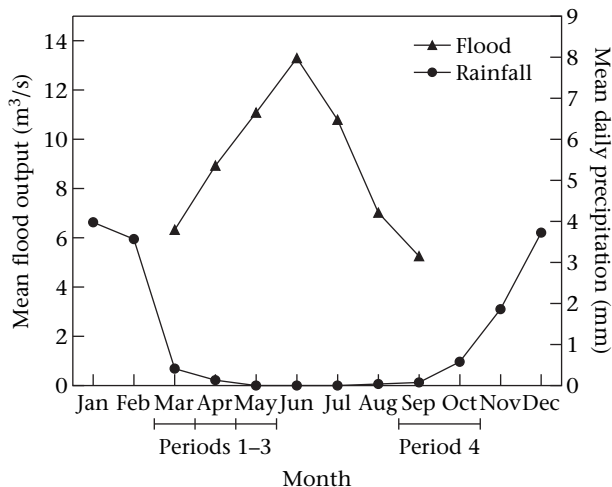
(faecal extract pool, $N = 6$). All samples were run in duplicate and mean concentrations are expressed in ng/g.

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 of peak excretion, we assumed a 24-h delay between faecal hormones and the discrete social events that define our time periods (i.e. male take-overs).

Behavioural Data

Behavioural data were collected from focal animal samples (10 min) on all adults in the group (Altmann 1974). During the four periods described here (February–October 2002), 1510 focal animal samples were conducted on all adults, for a mean of 6.3 h of observation time per individual or 1.6 h per individual per time period. Because we selected individuals for sampling from a randomized list without replacement, sampling was distributed evenly within and across observation periods.

'Grooming' interactions included all grooming bouts (grooming or being groomed) separated by more than 2 min. 'Aggressive' interactions included threat signals (e.g. eyelid threat, lunging, slapping the ground, 'open-mouth' display, threat vocalizations), and overt physical attack (biting, chasing, hitting). We examined both male aggression directed towards females and female–female aggression. We had no observed occurrences of immigrant male aggression directed towards infants. Intersexual grooming and aggression were only scored during focal animal sampling. For chi-square analyses, all acts of grooming or aggression were pooled across individuals for each time period and standardized by number of individuals and observation time.

We also noted any occurrences of male–male aggression. Because male–male aggression was both rare and highly conspicuous (Kitchen et al. 2003), we recorded these interactions using ad libitum rather than focal animal sampling. We calculated the rate of male–male aggression by dividing the number of aggressive interactions by the total number of hours spent with the group for that period.

Assessment of male–female friendships

Whenever a female was lactating we noted whether she had a male 'friend'. In this population, friendships have only been observed between males and lactating females (Palombit et al. 1997). A male friend was identified as any male with whom a lactating female had significantly more 'friendship' interactions (i.e. grooming, approaches, tolerance for infant handling) as compared with any other male (chi-square: $P < 0.05$). Because the duration of each period was relatively short (~ 1 month), more quantitative measures of friendship (as defined in Palombit et al. 1997) were not possible. Of the eight lactating females observed during the immigrant male take-over period, three had a male friend and five had no male friend.

Figure 1. Mean flood output (m^3/s) and daily precipitation (mm per day, based on monthly mean) in the Okavango Delta. Flood data were gathered over a 13-year period by the Water Affairs Department of Botswana. Precipitation data were gathered between 1999 and 2003 at a central location within the baboons' home range. Data points represent means for each month. Bars below the figure represent the sample periods for this study: 1 = Stable period (before), 2 = Natal male take-over, 3 = Immigrant male take-over, 4 = Stable period (after).

Data Analysis

We used a general linear model (GLM) to assess the effects of age, rank and reproductive stage on faecal hormone measures. For the GLM we entered all hormone samples into the analysis. For all subsequent analyses, we calculated a mean hormone value for each female (when more than one faecal sample was available) before calculating the mean for each time period. Nonparametric statistics were used for subsequent analyses. All statistical tests were two tailed, with the statistical threshold set at $P = 0.05$. All tests were conducted using the SPSS statistics package.

RESULTS

Female Glucocorticoids, Age, Reproductive Stage and Dominance Rank

We first assessed the relationship between female GCs and age, reproductive stage, dominance rank and time period. Our corrected model explained 46.3% of the variance in GC measures ($F_{60,196} = 1.95$, $P < 0.001$). Of the factors entered into the analysis, reproductive category and time period had a significant effect on fGC levels ($F = 3.72$, $P < 0.05$ and $F = 4.21$, $P < 0.01$, respectively). There were no significant interactions between any of the factors. Similarly, there was no obvious relationship between female fGC concentration and dominance rank (least squares regression: $R^2 = 0.05$, $P = 0.38$).

Subsequent analysis of reproductive stage and fGC measures showed that pregnant females had higher fGC levels than either cycling or lactating females and that this difference approached statistical significance (Kruskal–Wallis test: $\chi^2_2 = 5.83$, $P = 0.054$). During the course of a normal mammalian pregnancy, ovarian hormones stimulate the hypothalamic–pituitary–adrenocortical (HPA) axis, causing maternal GC concentrations to increase steadily throughout pregnancy, peaking during the third trimester at about two to three times that of nonpregnant values. Thus, pregnancy is a transient period of relative hypercortisolism (Taylor 2001; Mastorakos & Ilias 2003). It is not surprising, therefore, to find that fGCs levels were elevated in pregnant females.

Female Glucocorticoids and Changes in the Male Hierarchy

Table 1 shows individual mean fGC concentrations for cycling and pregnant and lactating females. Across the four time periods (stable, natal male take-over, immigrant male take-over, and stable), cycling females showed no significant differences in fGC concentrations (Kruskal–Wallis test: $\chi^2_3 = 4.58$, $P = 0.206$). This was not true, however, of pregnant and lactating females. These females showed significant differences across periods ($\chi^2_3 = 22.91$, $P < 0.001$), with higher fGC concentrations during the immigrant male take-over period ($P < 0.01$) compared with the natal male take-over and stable periods (Fig. 2). However, in no case did a pregnant female abort her infant.

Table 1. Mean faecal glucocorticoid concentrations (ng/g) of pregnant/lactating and cycling chacma baboons across the four time periods*

	Period of time							
	Stable (before)		Natal male take-over		Immigrant male take-over		Stable (after)	
	Mean ± SE	N	Mean ± SE	N	Mean ± SE	N	Mean ± SE	N
Pregnant/lactating females								
SL					118.57 ± 33.55	2	77 ± 13.78	7
PM	122.82 ± 4.89	2	113.89 ± 8.36	3	117.67 ± 8.31	3	86.17 ± 9.72	7
SR	83.33 ± 27.96	2	164 ± 17.35	2	215.31 ± 91.08	2	74.73 ± 9.59	7
CT	127.78 ± 17.25	3	105.27 ± 50.40	2	241.03 ± 0	1	85.88 ± 11.46	7
HL	121.19 ± 7.89	2	106.40 ± 35.64	4	121.04 ± 16.88	4	82.63 ± 12.34	7
HS	73.68 ± 13.07	3	80.98 ± 14.42	4	103.84 ± 16.88	4	78.38 ± 15.21	7
LK	113.57 ± 35.91	3	80.58 ± 6.02	4	184.84 ± 15.56	4	71.98 ± 5.96	7
NI	137.08 ± 56.87	2	67 ± 14.98	3	145.57 ± 25.43	3	94.81 ± 17.78	3
RS	117.26 ± 26.78	2	62.79 ± 17.05	3	115.40 ± 18.95	2	110.67 ± 16.65	6
AC	58.55 ± 5.09	3	94.13 ± 14.43	4	155.57 ± 40.66	2	82.32 ± 9.97	7
BL	136.51 ± 46.83	3	63.21 ± 3.44	2	127.73 ± 35.21	4	80.73 ± 18.43	7
JK	129.41 ± 27.38	3	108.21 ± 51.46	2	169.45 ± 0	1	100.26 ± 16.44	7
CP	124.69 ± 15.11	3	114.86 ± 31.50	3	124.48 ± 34.11	2	90.15 ± 15.97	7
Mean ± SEM	112.16 ± 23.75		96.78 ± 22.09		151.83 ± 25.26		86.56 ± 13.29	
Cycling females								
CL	149.53 ± 23.20	3	119.11 ± 28.64	3	102.21 ± 0	1	101.81 ± 18.84	6
LM	141.74 ± 17.35	2	69.57 ± 8.45	3	102.72 ± 18.29	4	118.42 ± 10.94	2
HN	89.11 ± 0	1	76.15 ± 12.99	4	140.27 ± 11.38	2	67.37 ± 9.51	5
CH	116.88 ± 21.89	3	89.44 ± 22.11	2	111.97 ± 9.26	2	108.23 ± 17.81	7
JN	110.44 ± 21.35	2	100.26 ± 6.18	3	121.74 ± 12.43	3	151.57 ± 23.5	6
Mean ± SEM	121.54 ± 16.76		90.91 ± 15.67		115.78 ± 10.27		109.48 ± 16.12	

*Females are listed in order of descending rank (i.e. SL is the highest-ranking female).
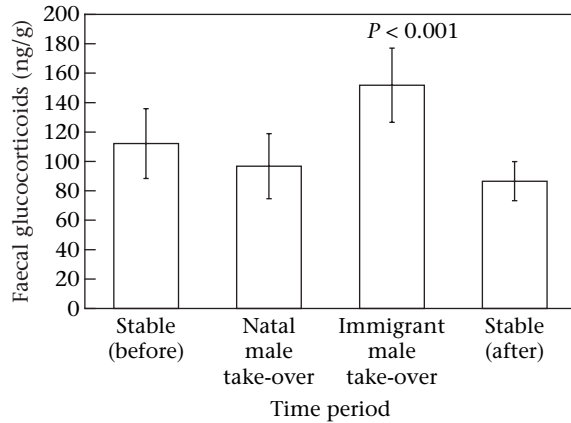
Figure 2. Mean faecal glucocorticoids ($+$SEM) for pregnant and lactating females across four time periods: (1) when the male dominance hierarchy was stable; (2) when a natal male rose to the alpha rank position; (3) when an immigrant male rose to the alpha rank position; and (4) when the male dominance hierarchy again became stable. Periods 1–3 are sequential in time, whereas period 4 follows a 3-month gap in hormone collection (see text for details). All hormone values are expressed as ng/g. For each period, $N = 13$ females.

Because our data set was too small to control for the number of pregnant females in each trimester in each time period, we removed pregnant females from the analysis altogether and ran the analysis again. With pregnant females removed, the results did not change ($\chi^2_3 = 16.33$, $P < 0.01$); lactating females still had the highest fGC concentrations during the immigrant male take-over period.

Results suggest, therefore, that the rise of a natal male to the alpha male position had little effect on fGC concentrations in pregnant and lactating females. In contrast, the take-over of the alpha position by a recent immigrant appeared to cause a significant elevation in fGC metabolites.

Female Glucocorticoids and Behaviour

One possible explanation for the increase in fGC metabolites among pregnant and lactating females during the immigrant male take-over period is that these females became the targets of increased aggression. This, however, was not the case. We found that incidents of male aggression towards pregnant and lactating females did not differ significantly from random across time periods (chi-square: $\chi^2_3 = 2.49$, $P = 0.48$; Fig. 3).

When we narrowed our focus to the immigrant male take-over period and examined only the incidents of aggression directed by the two immigrant males (BG and GM) towards pregnant and lactating females, we found that they did show higher rates of aggression than other males during this period (BG: 0.117 per min, GM: 0.125 per min, mean for all other males: 0.027 per min). However, both immigrant males' rates of aggression fell within the range of variation for other resident males when data from all time periods were included (range 0.055–0.197). In fact, the male who directed the most
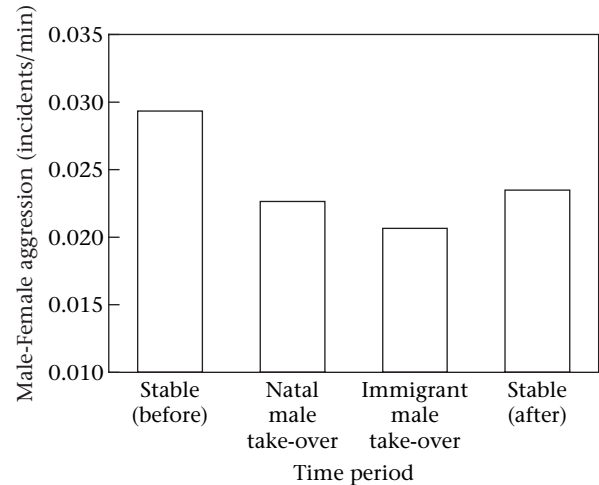

Figure 3. Rates of male aggression (incidents per minute) directed towards pregnant and lactating females across four time periods. Rates are based on pooled data for all individuals standardized by number of individuals and total observation time (for chi-square analysis).

aggression towards pregnant and lactating females (0.197 per min) was one of the lowest-ranking males in the group and had been resident for over 10 years. Immigrant males did not direct aggression preferentially towards pregnant and lactating females; targets of immigrant male aggression were equally likely to be cycling, pregnant or lactating females (Fisher's exact test: $P = 0.461$). Moreover, the specific females targeted by the immigrant males did not manifest higher fGC levels than females who were not targeted (Mann–Whitney U test: $U = 25.00$, $N_1 = 6$, $N_2 = 12$, $P = 0.303$).

Likewise, aggression rates among females were not elevated during the immigrant male take-over period. Rates of female aggression initiated or received by pregnant and lactating females did not differ from random across time periods (chi-square: $\chi^2_3 = 0.85$, $P = 0.839$; Fig. 4). Indeed, rates of female–female aggression for pregnant and lactating individuals were actually lowest during the immigrant male take-over period.

We also examined whether elevated levels of fGCs during the immigrant take-over period might have been related to changes in female grooming rates (directed or received). We found that grooming rates among pregnant and lactating females across time periods did deviate significantly from random, with significantly lower grooming rates during the immigrant male take-over period (chi-square: $\chi^2_3 = 34.16$, $P < 0.001$). However, cycling females showed a similar pattern with lower grooming rates during the immigrant male take-over period ($\chi^2_3 = 12.23$, $P < 0.001$; Fig. 5). Because rates of grooming declined for both pregnant and lactating females, who showed a rise in fGC metabolites, and cycling females, who did not, it seems unlikely that changes in grooming patterns strongly influenced increases in fGC measures.

Rates of male–male aggression across the four time periods were not randomly distributed (chi-square: $\chi^2_3 = 9.27$, $P < 0.05$). Elevated levels of male–male aggression were observed not only during the period following
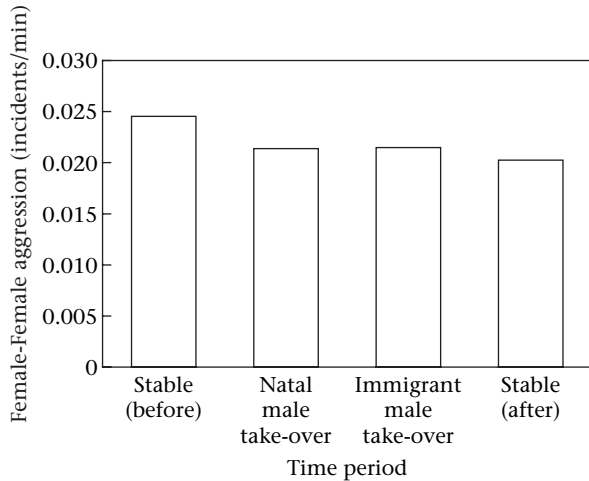
Figure 4. Rates of female aggression (incidents per minute) received or inflicted by pregnant and lactating females across four time periods. Legend as in Fig. 3.

Figure 6. Rate of male–male aggression (incidents per hour) across four time periods. Bars represent total number of incidents observed (ad libitum sampling) divided by total number of observation hours.

the immigrant male take-over but also during the natal male take-over and the initial stable period (Fig. 6). Rates of male–male aggression were lowest during the stable period (period 4) after the immigrant male take-over. In this population, stability in the male alpha rank position is relatively transient (Hamilton & Bulger 1990; Bulger 1993). Therefore, higher rates of aggression during the first three periods may be more representative of male aggression levels for this group.

Although we did not measure food availability in this study, the sharp increase in fGC levels among pregnant and lactating females from the month of the natal male take-over to the month of the immigrant male take-over appeared unlikely to result from a decrease in food availability or an inc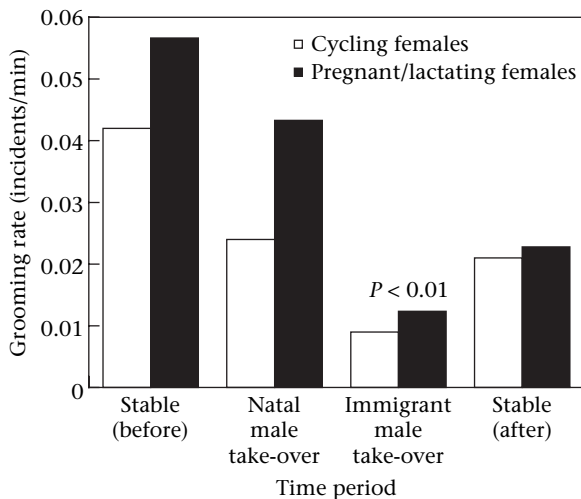rease in energy expenditure related to foraging. Both periods occurred after the rainy season and before the arrival of the annual flood (Fig. 1). Moreover, in both periods, rates of supplants, which provide an indirect measure of food competition, were almost identical. During the month of the natal male take-over, pregnant and lactating females were supplanted an average of 4.0 times per hour. In the subsequent month, after the immigrant male take-over, the same females were supplanted an average of 4.5 times per hour (Wilcoxon signed-ranks test: $T = 42.0$, $N = 13$, $P = 0.820$).

In summary, increases in fGC measures for pregnant and lactating females were associated with the arrival of the immigrant males but not with any other behavioural variables.

Female Glucocorticoids and Male–Female Friendships

To test whether a friendship with a resident male might have dampened the stress response of lactating females during the immigrant take-over period, we examined fGC profiles and the male–female friendships for all lactating females from whom we had hormone samples. Three females had a male friend during this period, and five did not. The percentage rise in fGC metabolites during the immigrant male take-over period was calculated as the difference between stable fGC concentrations (a mean from both stable periods) and the immigrant male take-over fGC concentrations, divided by the stable fGC concentration, multiplied by 100.

Lactating females who had a male friend during the immigrant male take-over period had significantly lower fGC concentrations than females without a male friend (Mann–Whitney U test: $U = 0.00$, $N_1 = 3$, $N_2 = 5$, $P < 0.05$). The mean fGC rise for females with a male friend was 38.9% (range 15.7–59.8%), compared with 57.9% for females without a friend (range −2.8–136.4%).

Figure 5. Rates of female–female grooming (incidents per minute) for females of different reproductive stages across four time periods. Legend as in Fig. 3.
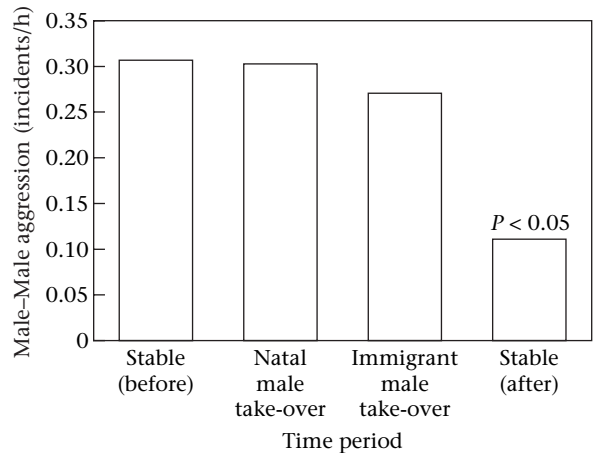
Although sample sizes were too small to permit statistical analysis, there were no apparent differences in fGC levels between lactating females with and without a male friend during either the natal male take-over period or the two stable periods (Fig. 7). Only during the immigrant male take-over period did females without a friend show sharply increased fGC concentrations. By contrast, females with a male friend maintained fGC levels that were roughly the same as those shown by all lactating females during the other three time periods.

Females with a male friend held significantly higher dominance ranks than females without a male friend ($U = 3.00$, $N_1 = 3$, $N_2 = 10$, $P < 0.05$). This result was not surprising, since previous observations had suggested that females in this population often compete for access to male friends (Palombit et al. 2001). To determine whether dominance rank or the availability of a male friend was a better predictor of dampened fGC concentrations, we added pregnant females (who also showed elevated fGC levels during this period) to our analysis and examined this larger sample to determine whether dominance rank had an effect on (1) the rise in fGC from the stable to the immigrant male take-over period, or (2) overall fGC concentrations during the immigrant male take-over period. We found no significant rank effect among pregnant and lactating females combined, for either the rise in fGC metabolites (least squares regression: $R^2 = 0.01$, $P = 0.72$) or overall fGC concentrations ($R^2 = 0.01$, $P = 0.82$). These results suggest that, although high-ranking lactating females may have experienced preferential access to male friends, the lower fGC levels manifested by these females were due less to their high dominance ranks per se than to their friendships with males.
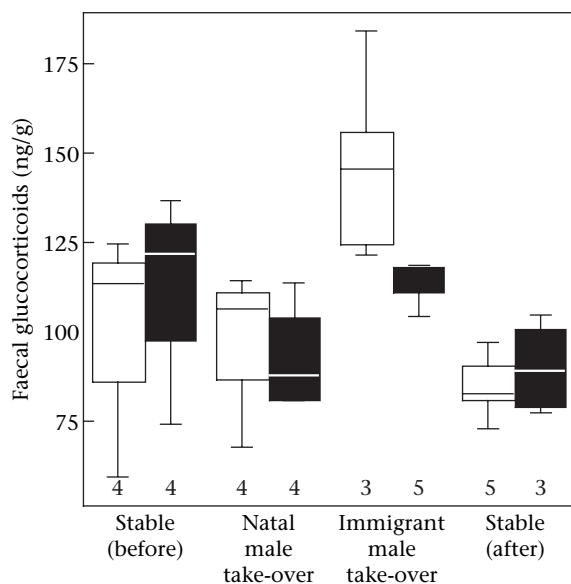
DISCUSSION

In a study of South African chacma baboons living at a higher latitude (34°27′S) and in a more seasonal environment than the Okavango population, Weingrill et al. (2004) found that both pregnant and lactating females had elevated GC measures compared with cycling females. This contrast was particularly evident during the winter, when food was scarce. In the Okavango, pregnant females also manifested higher concentrations of GCs, although this difference did not quite reach statistical significance. The short duration of this study did not permit us to examine seasonal variation in GC measures. We suspect, however, that future research will reveal seasonal effects to be minimal, due to the unique ecology of the Okavango Delta. The annual flood generally arrives in the delta soon after the summer rains cease. There is, therefore, a relatively constant source of water, and provided that the flood and/or rains do not fail, there is nearly always at least one tree species in fruit (Ellery et al. 1993; Roodt 1998). As a result, there does not appear to be as extreme a seasonal transition between periods of food abundance and scarcity for the Okavango population as has been described for other primate populations (Lee 1987; Hauser & Fairbanks 1988; Hill et al. 2003; Alberts et al., in press), and pregnant and lactating females may not be under as much nutritional stress.

Our preliminary data suggest that female baboons' GC concentrations were affected most strongly by an interaction between reproductive state and the arrival of potentially infanticidal immigrant male. When a natal male rose to the alpha position, few females showed an increase in GC measures. By contrast, when two immigrant males entered the group and quickly rose to the alpha and beta positions, GC metabolites rose significantly, but only among lactating and pregnant females. Furthermore, the stress response of pregnant and lactating females was not associated with elevated aggression levels. Taken together, these observations suggest that lactating and pregnant females were responding to the threat of infanticide rather than male social instability. Long-term data on the study group indicate that natal males rarely, if ever, attempt infanticide, whereas infanticidal attempts from immigrant males who rise to the alpha position are common (Palombit et al. 1997). In the latter case, males target only the infants of lactating females.

The specificity of females' stress response can be compared with that of adult males during the same time periods. In contrast to females, the fGC concentrations of males were significantly elevated during both periods of instability, the natal male take-over period and the immigrant male take-over period, as well as during the initial 'stable' period (Bergman et al., in press). Recall that a natal male was quickly rising in the male hierarchy during this initial period. Male–male rates of aggression showed a similar pattern, with elevated levels during all periods except the final stable period. Therefore, males appeared to be responding to all instability in the higher ranks of the hierarchy, not just the arrival of an unfamiliar male, a result that has also been found in other baboon populations (Sapolsky 1993b).

Figure 7. Faecal glucocorticoid concentrations (mean ± SE, ng/g) for lactating females with a male friend (□) and without a male friend (■) during the four periods. Numbers on the X axis indicate the number of females included in the analysis.

Several authors have suggested that certain sorts of social relationships, like bonds among female kin or male–female friendships (e.g. Palombit et al. 1997; Silk et al. 1999, 2003), may buffer and protect females against the effects of stressful events like the arrival of a new alpha male. We found no evidence that female–female grooming affected the stress response of pregnant and lactating females during the immigrant male's take-over. During this period, rates of grooming declined among all females, including those who were sexually cycling and showed no increase in GC concentrations.

In contrast, we found that lactating females that had a male friend showed a less marked increase in GCs and had significantly lower GC measures overall during the immigrant male take-over period than did lactating females without a friend. Heterosexual friendships in chacma baboons appear to function as counterstrategies against the threat of infanticide. Both observational and experimental evidence indicate that male friends invest heavily in the defence of lactating females and their infants, and interventions by male friends considerably reduce the likelihood of infant injuries or deaths (Palombit et al. 1997, 2000). It seems likely that lactating females that have friends may perceive themselves to be at a reduced risk of infanticide and therefore manifest lower GC concentrations.

While females with male friends were higher-ranking than those without friends, dominance rank alone did not appear to be responsible for these females' lower GC measures, because high-ranking pregnant females did not show similar attenuated stress responses. Rather, it appears that high-ranking females were able to compete more successfully for access to a male friend (Palombit et al. 2001), and that these friendships may have dampened the stress response during the immigrant male take-over.

An alternative explanation for the reduced GC levels shown by lactating females that had friends is that these females enjoyed preferential access to food resources. If this were true, hormonal differences between females with and without male friends should have been evident in all time periods. In fact, however, the difference emerged only during the immigrant male take-over period.

It is also possible that the high GC levels shown by pregnant and lactating females during the immigrant male take-over period resulted from increased energetic expenditure, reduced feeding opportunities, or food scarcity during this time. Energy expenditure is suspected to lead to increased physiological stress and elevated GC measures in a number of primates, including callitrichids and male chimpanzees, Pan troglodytes (Bercovitch & Ziegler 2002; Muller & Wrangham 2004). Although we did not collect data on food abundance and feeding rates, it seems doubtful that these factors contributed significantly to the increase in GC concentrations. First, elevated GC measures in dominant male chimpanzees are associated with high rates of aggressive activity (Muller & Wrangham 2004). In contrast, the increased GC measures in pregnant and lactating female baboons were not correlated with an increase in aggression given or received. Second, GCs in pregnant and lactating females increased

significantly over a period of only one month. It seems unlikely that food abundance decreased dramatically over such a short period, particularly because there were no seasonal changes in rainfall or temperature during this time. Both the natal male take-over period (when GCs were low) and the immigrant male take-over period during the next month (when GCs rose significantly) occurred after the rainy season, before winter, and before the arrival of the annual flood. Third, during both the natal male take-over and the immigrant male take-over period, pregnant and lactating females were supplanted at approximately equal rates, suggesting that food competition was similar in both months. Thus, although it remains possible that increased energy expenditure, food competition and disruptions in feeding may have contributed to elevated GC concentrations in pregnant and lactating females, they are unlikely to have been the sole or most significant causes.

Previous research on the relationship between GC measures and dominance rank in female monkeys has yielded mixed results. Some studies have found that low rank is correlated with high GCs (Gust et al. 1993; Shively et al. 1997), a pattern that replicates the data from many studies of adult males (Sapolsky & Ray 1989; Ray & Sapolsky 1992). Others, however, have found that low rank is correlated with low GCs (Saltzman et al. 1998), and still others have found no consistent relationship (Abbott et al. 1997; Smith & French 1997; Stavisky et al. 2001). Results from this study suggest that female GC measures are the result of a complex interaction between several factors, including dominance rank, reproductive state, social events involving other group members, and the existence (or lack) of social relationships that might attenuate a female's stress response. In this respect, our data are consistent with those of Alberts et al. (1992), who found that the immigration of a highly aggressive, dominant male baboon prompted a sharp increase in serum cortisol levels among adult females, and Abbott et al. (2003), who found that decreased opportunities for social support resulted in higher relative cortisol levels.

Three months following the immigrant male take-over, the GC measures of pregnant and lactating females were indistinguishable from the time periods prior to all male take-overs. This return to 'baseline' appears to challenge the hypothesis that elevated GC metabolites among lactating females occurred as a result of the infanticidal threat posed by immigrant males because all of the pregnant and lactating females were still potentially vulnerable to infanticide. However, since not all immigrant males commit infanticide and since the stress response itself may be harmful (particularly if it is a proximate mechanism for fetal loss), it should be advantageous for females to discriminate between potentially infanticidal and noninfanticidal immigrant males (Huck 1984). During the year following the immigrant male's arrival, four of 26 infants under the age of 1 year died. Two of these deaths followed the death of the infant's mother and two are believed to have been caused by predation. While we cannot say for certain that the two latter infant deaths were not due to infanticide, the overall infant mortality rate for this year (0.15) was considerably

less than the 10-year mean (0.21). The low rate of infant mortality, together with the lack of any observed infanticidal attempts, strongly suggests that this immigrant male was noninfanticidal. Evidence that female GCs returned to baseline levels after a few months suggests that females are able to discriminate between males that represent an infanticidal threat and males that do not.

A lack of predictability has been shown to compound the effects of stress (Hennessy et al. 1977; Dess-Beech et al. 1983; Wingfield & Ramenofsky 1997). Due to the high rate of infanticide in this population, the arrival of an immigrant male represents an unpredictable threat for resident females. However, as the threat appears to diminish or even become nonexistent, a return to baseline glucocorticoid levels is expected. To test this last hypothesis, we are now collecting faecal samples from a larger sample of females across additional immigrant male takeover periods, some with and some without evidence of male infanticide. We predict that when the immigrant male is infanticidal, females will manifest higher elevations in GC levels than those observed in this study and that the return to baseline levels will not occur until after infants are weaned.

Acknowledgments

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